

TEMPERATURE TOLERANCES IN
THE AMERICAN ALLIGATOR
AND THEIR BEARING ON
THE HABITS, EVOLUTION,
AND EXTINCTION OF
THE DINOSAURS

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AND CHARLES M. BOGERT

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INTRODUCTION

THIS PAPER IS THE LOGICAL OUTGROWTH of an earlier paper by one of the present authors (Cowles) entitled "Additional implications of reptilian sensitivity to high temperatures" (1940) and a resultant exchange of correspondence between two of us (Cowles and Colbert) in which various aspects of dinosaurian extinction were discussed. As a result of some extended work on the temperature tolerances in desert lizards, Cowles speculated in his paper on the possibility that the great extinction of reptiles at the end of Mesozoic times may have been due in no small part to an increase in the temperature of the environment whereby the upper limits of tolerance in these reptiles might have been exceeded. Colbert took issue with this proposal (in correspondence) by pointing out the fact that the geologic evidence does not particularly favor the idea of a temperature rise toward the end of Cretaceous time but rather, if anything, a certain amount of lowering in environmental temperatures. In other words, it seems possible that there was a change, during the late Mesozoic to early Tertiary transition, from tropical to subtropical and temperate conditions in the middle and higher latitudes, and that this change marked the end of the widely spread equable environment which for such a long time had been characteristic of the later part of the Mesozoic Era. However, Cowles felt that the interpretation of geologic evidence for a moderate increase in temperature might be impossible, and while the nature of flora and its distribution are less difficult to assay in terms of temperature, such evidence might not reveal thermal changes of the order of magnitude (a few degrees) that might be required to effect the extermination of the dinosaurs. It was admitted by both participants in the discussion that this is a subject about which it is difficult to particularize, so that much of what is said must be more or less in the realm of "legitimate speculation."

The point came out during discussions that many of the conclusions previously arrived at as a result of temperature experiments on lizards and snakes may not

properly be applicable to the problem of dinosaurian extinction.

Modern lizards and snakes are for the most part relatively small animals, living close to the ground. Therefore they are greatly influenced by substratum temperatures and by heat reflection from the surface of the earth. The adult dinosaurs were for the most part very large animals, and most of them had their bodies raised above the ground to such an extent that substratum temperatures and heat reflections were probably effectual heating factors chiefly during their juvenile stages. As far as the adults of smaller species are concerned, these factors would become increasingly important and would be most effective in the smallest species.

Living lizards are generally of such small size that they bear little resemblance to the large dinosaurs. They respond rapidly to changes in the environmental temperature, for there is a relatively small amount of body mass to be heated or cooled. Furthermore, their remote relationships to the dinosaurs, and differences in the proportions of their bodies, their capacity for a rapid change in albedo (reflection coefficient), and their great tolerance to high temperatures (in diurnal species) combine to render them less suitable material for comparison than might be wished. However, because temperature changes in an ectotherm are predominantly the result of physical rather than physiological effects and therefore depend primarily on albedo and surface-mass relationships, there is some validity in a general comparison between the heating rates observed in a large lizard and a very small, or young dinosaur. This similarity should hold even more strongly for the early stages in the growth of a crocodilian. The adult dinosaurs possessed of great body masses must have been slowly affected by temperature changes, but the young, with body masses comparable to some modern reptiles, especially the crocodilians, would have been rapidly affected. It may be surmised that where days and nights are of equal lengths in the tropical zone the adults probably were subjected to

much smaller fluctuations in body temperature during each twenty-four-hour period because of this surface-mass factor.

In the light of their phylogenetic relationships and their probable physiologic similarity, Colbert suggested that it would be much to the point, as far as speculating upon the dinosaurs is concerned, to make some temperature experiments with crocodilians. In the first place these are relatively large reptiles, and while those available for study are almost never comparable with the larger dinosaurs in size, nevertheless the surface-mass ratios of individuals would approximate those of dinosaurs at the earlier stages of growth through which these great reptiles of Mesozoic times must have passed. Experiments upon a fifty-pound crocodilian are likely to give more insight into responses of the adult dinosaurs and their juvenile stages than are experiments upon small snakes or lizards, even though there is still a tremendous size difference between a fifty-pound crocodilian and a five-, ten-, or twenty-ton dinosaur. Of course a one- or two-pound lizard may be larger than some of the newly hatched or newly born dinosaurs. However, the smaller animals provide less reliable information usable in direct comparison with large adult dinosaurs. Secondly, the crocodilians, being subtropical and tropical reptiles, live in environments that approximate most closely the temperature conditions under which the dinosaurs evolved and lived. However, in this connection it must be remembered that there is an important difference between the tropics and the temperate zone, namely, the seasonal variations in the proportion of light between night and day. Thus a tropical climate within the temperate zone during the summer would have a disproportionate number of daylight hours during which heat could be absorbed, accompanied by short nights with fewer hours for heat loss. This is the chief explanation for the much lower maximum temperatures recorded within the tropical zone as compared with maximum temperatures in the temperate zone at present time. Finally, the crocodilians have the great merit of being closely related to the dinosaurs, for they are

the only surviving archosaurians. In their osteological and myological structure they show throughout their anatomy close relationships with the dinosaurs; therefore it may be supposed that a similar physiological relationship is to be expected.

Hence, we welcomed an opportunity to spend some time during the summer of 1944 at the Archbold Biological Station, located near Lake Placid, Florida. Here, we thought, was a chance to work upon a crocodilian, the American alligator, in its natural environment. Moreover, this environment probably approximates rather closely the environment in which the late Cretaceous dinosaurs lived. For in southern Florida, as was the case in late Cretaceous times, there is a mixture of palms and cycads on the one hand, and pines and hardwood trees on the other, a mixture denoting subtropical rather than true tropical conditions. This type of floral association in Cretaceous time may have been a partial result of combined phylogenetic and climatological effects. However, since the type of vegetational association denotes a temperate zone-subtropical climate rather than tropical conditions, a visit to the Archbold Biological Station was especially opportune since some attempt at a solution of the problems of temperature tolerances in the alligator could be made there. It was felt that this work would in turn throw some light upon temperature tolerances in the long since extinct dinosaurs.

For our opportunity to visit the Archbold Biological Station we wish to acknowledge aid from three sources, namely, the American Museum of Natural History, the University of California, and the Archbold Expeditions. To Mr. Richard Archbold and his associates at the Archbold Biological Station we wish to express our appreciation for facilities and aid in carrying out our work during the time we were working on the problem of temperature tolerances in the alligator and in other reptiles. We are also greatly indebted to Prof. A. D. Moore of the University of Michigan for his searching criticisms of the preliminary manuscript and his numerous helpful suggestions.

ANIMALS USED IN THE EXPERIMENTS

WHEN WE ARRIVED at the Archbold Biological Station there were only two alligators on hand. One of these was small, about 2 feet in length, the other a fairly large animal almost 7 feet long. Soon after we arrived we managed to catch an alligator about $2\frac{1}{2}$ feet long, and with these three animals some preliminary experiments were made. It became immediately apparent, however, that to carry out the work a graded series of animals was needed, and with the limited amount of time at our disposal it was certain that we would be unable to catch the necessary number of animals of the proper sizes, so arrangements were made to have these animals supplied by Mr. Ross Allen of Ocala, Florida. Mr. Allen gave the fullest possible cooperation, and through him we were able to obtain 10 alligators, ranging in size from a newly hatched individual to an animal more than 5 feet in length. Thus, with these animals, together with the three already on hand, it was possible to make the experiments that had been planned with results that may be considered as of significant value. Of course it would have been advantageous to have had a much larger series, but considering the time limitations under which we were working we felt that the series used was about as large as it would be practical for us to handle. Such proved to be the case.

As said above, some preliminary experiments were made with the three alligators that were available shortly after we arrived at the Station. After we received the 10 alligators from Mr. Allen we used these, plus one of the original three, in the subsequent

experiments. The alligators were given numbers and marked so that they might easily be identified when we were working with them. The lengths and weights of the 13 alligators are given in table 1.

TABLE 1

ALLIGATOR NO.	LENGTH	WEIGHT
1	275 mm.	47.5 gr.
2	477	195.2
3	470	206.8
4	635	481.9
5	635	689.2
6	1010	2272.0
7	1010	3636.0
8	1090	4772.0
9	1190	5681.0
10	1130	5909.0
11	1510	13068.0
12	1981	24501.0
13	820	1497.0

In table 1 it is interesting to note the differences in weight between animals of approximately similar lengths. From an analysis of data presented by McIlheney (1935, pp. 113-114) it would seem to be apparent that there is a considerable amount of individual variation in weight and length among animals of the same age. Moreover, as shown not only by McIlheney's data, but also by this present series of animals, individuals of approximately the same length may differ appreciably in weight. These differences are within the ranges of normal individual variation and supposedly do not reflect abnormalities in growth or physical condition.

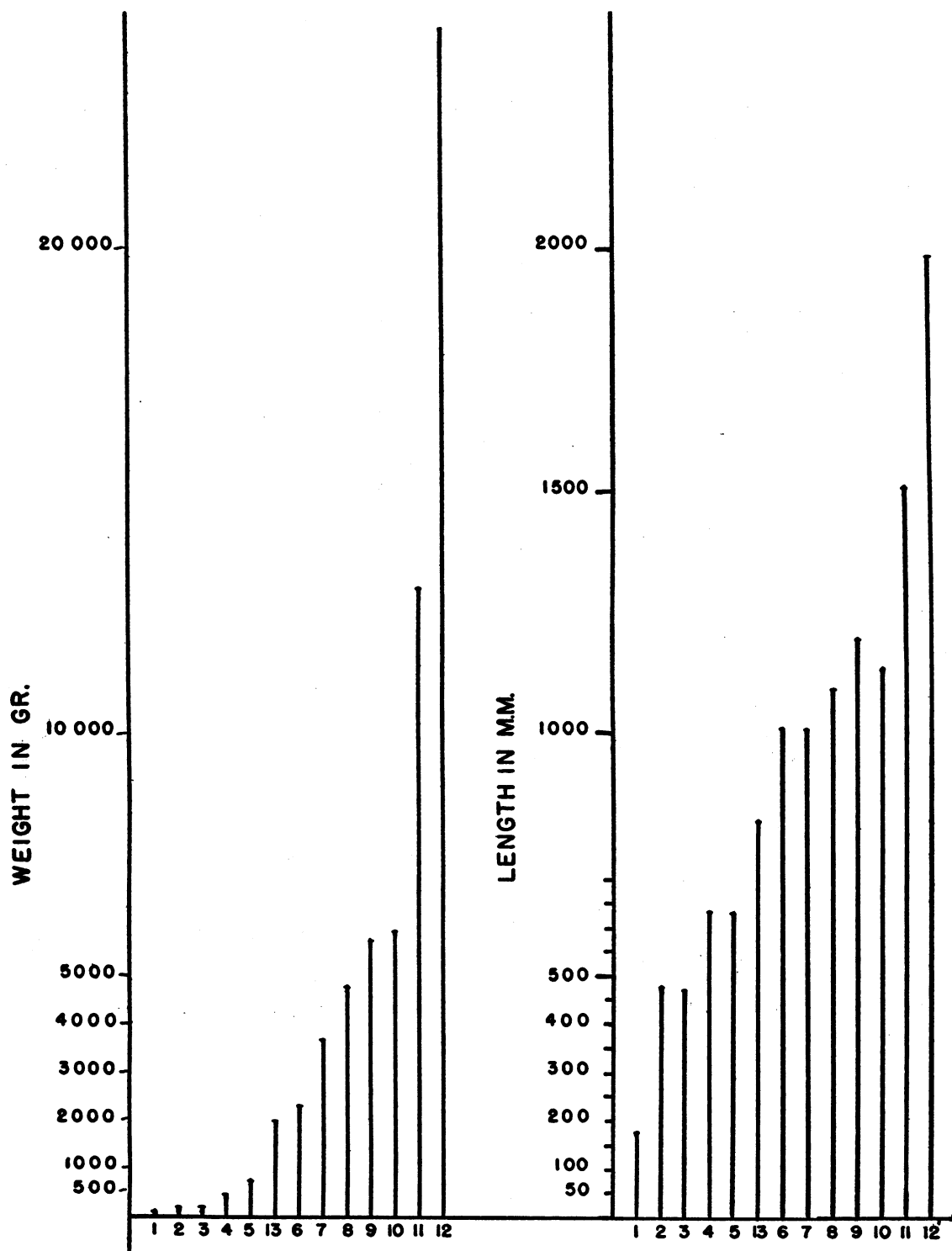


FIG. 1. Graphs to show weight (on left) and length (on right) of 13 alligators used in the experiments at the Archbold Biological Station. See table 1.

EXPERIMENTS ON TEMPERATURE TOLERANCES IN *ALLIGATOR MISSISSIPIENSIS*

1. TOLERANCE TO HEAT IN DIRECT SUNLIGHT

PURPOSE

THE PURPOSE OF THIS EXPERIMENT was to determine the responses of alligators to the heat of direct sunlight. How would animals of different sizes react when exposed to the heat of the sun? How rapidly would the body temperature rise in animals of different sizes and at what levels would it approach and reach the critical maximum?¹ What is the lethal temperature for the alligator?

TECHNIQUE

The technique for this experiment was very simple. The animals to be used were tethered by short strings or ropes to stakes driven into the ground. Cloacal temperatures were taken at stated intervals,² and simultaneously black bulb temperatures, taken in direct sunlight, were obtained.

¹ This is defined by Cowles and Bogert (1944, p. 277) as "the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death." It is also called the potential lethal.

² Thermometers used in taking cloacal temperatures were of a special type designed to give rapid readings within the range of 0° to 50° C. The stem was etched to permit readings to within 0.2 of a degree, and those used were checked for accuracy with standard thermometers. Care was taken to thrust the thermometer to comparable depths when taking cloacal readings.

When animals approached the critical maximum (after this was ascertained) they were removed to the shade and in some cases sprayed with water. During the later trials of this experiment cloacal temperatures were taken, not only while the animals were in the sun but also after they had been removed to the shade. In these cases air temperatures in the shade were also observed.

RESULTS

PRELIMINARY TRIALS

This was the first experiment attempted, and some preliminary trials were made with the three alligators first at hand, before the graded series was available. There were several reasons for making these preliminary trials. In the first place, it was desirable to "feel out" this technique, to see if things were going to work more or less as anticipated. Again, it was necessary to get some idea of the rate of temperature rise in animals placed in the sun in order that there might be some guide as to the manner and speed in which future trials should be made. Finally, it was important to learn the approximate critical maximum and lethal temperatures if future trials were to be made without unnecessary loss of materials—a real item when dealing with animals as difficult to obtain and as expensive as large alligators.

TABLE 2
FIRST OF PRELIMINARY TRIALS

General Conditions	Time	Cloacal Temperature Alligator No. 13	Notes
Aug. 21, 1944 Sun bright	10:10 A.M.	27.0° C.	Walked 95 ft. in 1 min. 52.6 sec.
	10:12	28.5	
	10:30	32.0	
	10:35	—	
	10:40	34.2	
	10:50	34.5	
	11:15	36.8	
	11:24	39.0	Walked 48.5 ft. in 55 sec.

TABLE 3
SECOND OF PRELIMINARY TRIALS

General Conditions	Time	Cloacal Temperatures Alligators			Notes
		No. 5	No. 13	No. 12	
Aug. 22, 1944 Sun bright to hazy	10:25 A.M.	26.5° C.	26.5° C.	29.0° C.	
	10:40	31.0	30.1	29.1	
	10:55	35.1	34.0	30.0	
	11:10	37.5	36.0	31.5	
	11:25	40.0	38.0	32.5	
	11:33	39.5	38.0	—	Lethal for no. 13
	11:37	39.0	—	33.5	
	11:50	—	—	34.5	
	1:00 P.M.	—	—	38.0	Lethal for no. 12

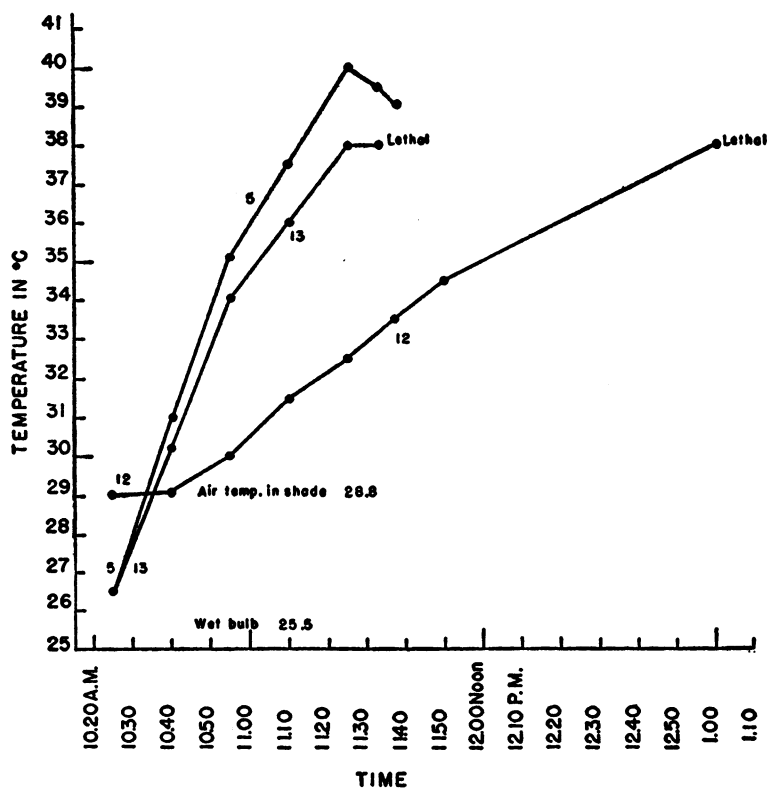


FIG. 2. Tolerance to heat in direct sunlight, second preliminary trial. Numbers indicate the animals used. See table 3.

TABLE 4
FIRST OF FINAL TRIALS

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators								
			No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 10	No. 11
Animals tethered on grass at 1:30 P.M.	1:40 P.M.	56° C.	31.0° C.	30.4° C.	30.6° C.	29.8° C.	31.0° C.	28.6° C.	30.2° C.	28.8° C.	28.3° C.
	1:50	59	36.8	36.4	37.0	34.0	33.2	31.3	32.0	31.5	29.8
	1:55	60	—	—	—	36.0	35.0	—	—	—	—
	2:00	62	—	—	—	—	—	34.2	34.4	33.7	31.7
	2:05	63	—	—	—	—	—	36.3	37.2	35.8	34.0
	2:12	—	—	—	—	—	—	—	37.5	37.0	34.5
	2:16	—	—	—	—	—	—	34.4	35.6	36.3	35.4
	2:26 ^a	—	—	—	—	—	—	32.3	33.0	34.5	34.9

^a Nos. 6, 7, 10, 11 removed to shade, sprayed with water from hose.

TABLE 5
SECOND OF FINAL TRIALS

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators								
			No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 10	No. 11
Sept. 5, 1944	9:30 A.M.	—	27.0° C.	27.1° C.	26.8° C.	27.9° C.	28.0° C.	28.4° C.	28.0° C.	28.5° C.	28.2° C.
Animals tethered on grass at 9:35 A.M.	9:40	46.5° C.	33.4	31.8	31.3	30.5	30.5	29.5	29.6	30.4	30.0
	9:45	51	33.5	33.5	33.0	33.7	31.0	30.5	31.0	31.2	30.2
	9:50	52	—	35.0	34.8	33.6	33.3	31.3	31.5	31.3	30.6
	9:55	52	—	—	—	—	—	31.9	31.8	32.2	30.8
	10:00	53	—	—	—	—	—	32.6	33.2	33.0	32.3
	10:05 ^a	56	—	—	—	—	—	—	—	—	32.0
	28.8 10:10	—	—	—	—	—	—	33.6	34.1	33.6	32.8
	— 10:15	—	—	—	—	—	—	33.9	34.0	34.0	33.0
	— 10:20	—	—	—	—	—	—	33.5	34.0	34.0	33.2
Air temp. in shade	29.4 10:25	—	—	—	—	—	—	33.2	33.7	34.0	33.3
	— 10:30	—	—	—	—	—	—	32.8	33.5	33.8	33.2
	— 10:35	—	—	—	—	—	—	32.6	33.2	33.5	33.2
	— 10:40	—	—	—	—	—	—	32.5	33.0	33.4	33.2
	— 10:45	—	—	—	—	—	—	—	—	—	33.0
	30.5 10:50	—	—	—	—	—	—	—	—	—	32.9
	— 11:00	—	—	—	—	—	—	—	—	—	33.0
	— 11:30	—	—	—	—	—	—	—	—	—	33.5

^a Nos. 6, 7, 10, 11 moved to shade, grass cool and wet.

FIRST TRIAL

The first trial was made with a single animal, no. 13, one of the smaller individuals. In this particular case the animal was allowed to roam freely on the pavement of a large plaza adjacent to the main building of the Biological Station. Body temperatures may have been affected to some degree by the fact that the animal was more active than it could have been had it been tethered. The data are in table 2.

At the time of the last reading the alligator was showing signs of great discomfort, and it was obviously at or near the critical maxi-

mum. It was rushed into the laboratory and placed in a tank of water, with the result that it revived.

SECOND TRIAL

In the second trial three animals were used, nos. 5, 13, and 12. These animals were tethered in direct sunlight, which alternated between bright and hazy.

At a temperature of 38° C., no. 13 died almost immediately. All efforts to revive this animal failed.

It was, therefore, decided to terminate trials in the future before the animals had reached this temperature. Accordingly at

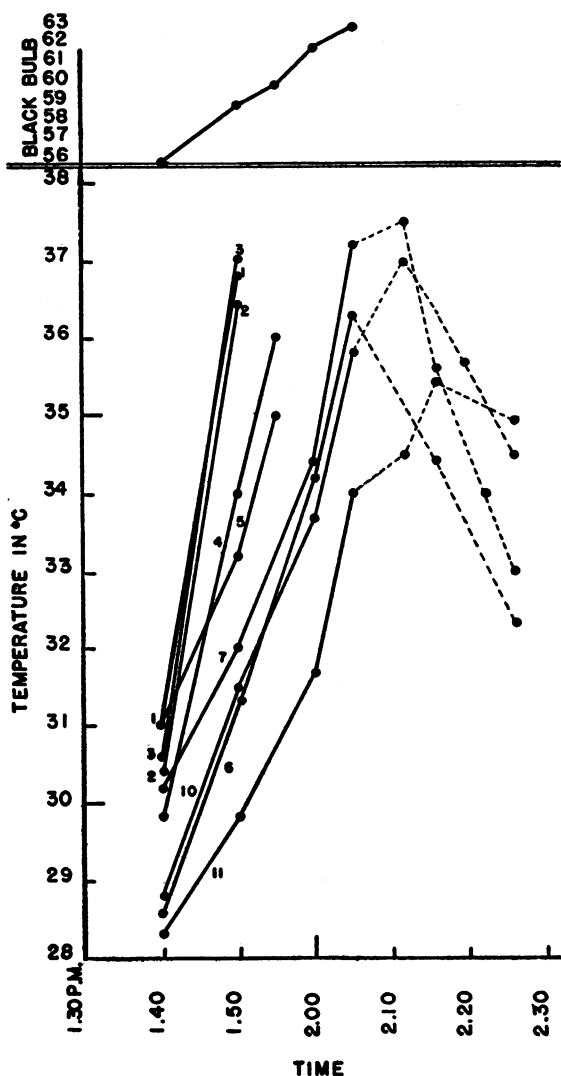


FIG. 3. Tolerance to heat in direct sunlight, showing rates of heat absorption and heat loss in alligators of various sizes. First trial. Numbers indicate the animals used. The solid lines show temperature rises during exposure to the sun; the dotted lines show fluctuations of temperatures after the removal of the alligators to the shade. See table 4.

11:50 A.M., when the big alligator had reached a temperature of 34.5°C ., it was tethered in the shade. Unfortunately the shade shifted and the animal moved about so that at 1:00 P.M. we found it in the sun. Its temperature was taken and was found to be 38.0°C ., so we immediately sprayed the alligator with water from a hose in an effort

to revive it. The animal seemed to revive, so it was removed to a big pool, with water at a nearly constant temperature of 26°C .- 28°C ., where we hoped that it would recuperate. The next morning, however, it was dead. What had happened, although we did not realize it at the time, was that the cloacal temperature of the animal continued to rise after it had been removed to the shade, so that the body temperature reached or passed the critical maximum and remained at this high stage for some time, with the result that the animal eventually died. This was owing to the fact that higher temperatures are first attained near exposed surfaces, and there is a time lag in the cloacal temperature build-up in large animals because of their great mass, a fact that was learned subsequently in our work with the graded series of alligators. From this it may be presumed that when the cloacal temperature had finally reached 38°C ., temperatures in the external portions of the body must have been considerably higher.

The results of this trial are shown in figure 2.

From these preliminary trials it was decided that the critical maximum for cloacal temperatures in larger specimens of *Alligator mississippiensis* is approximately 38°C ., while the lethal temperature is but slightly above this level.

FINAL TRIALS

The preliminary trials were made with three animals; the final trials (tables 4 and 5) were attempted with the graded series of alligators. The animals used were nos. 1, 2, 3, 4, 5, 6, 7, 10, and 11, the measurements and weights of which are given on page 335. In each trial the animals were placed in the sun simultaneously, temperatures were taken at short intervals, and none of the animals was allowed to reach the critical maximum of 38°C . In performing this experiment the animals were staked out in order, from the smallest to the largest, and cloacal temperatures were taken in this sequence. In this way approximately equal intervals were maintained between temperature readings on each individual.

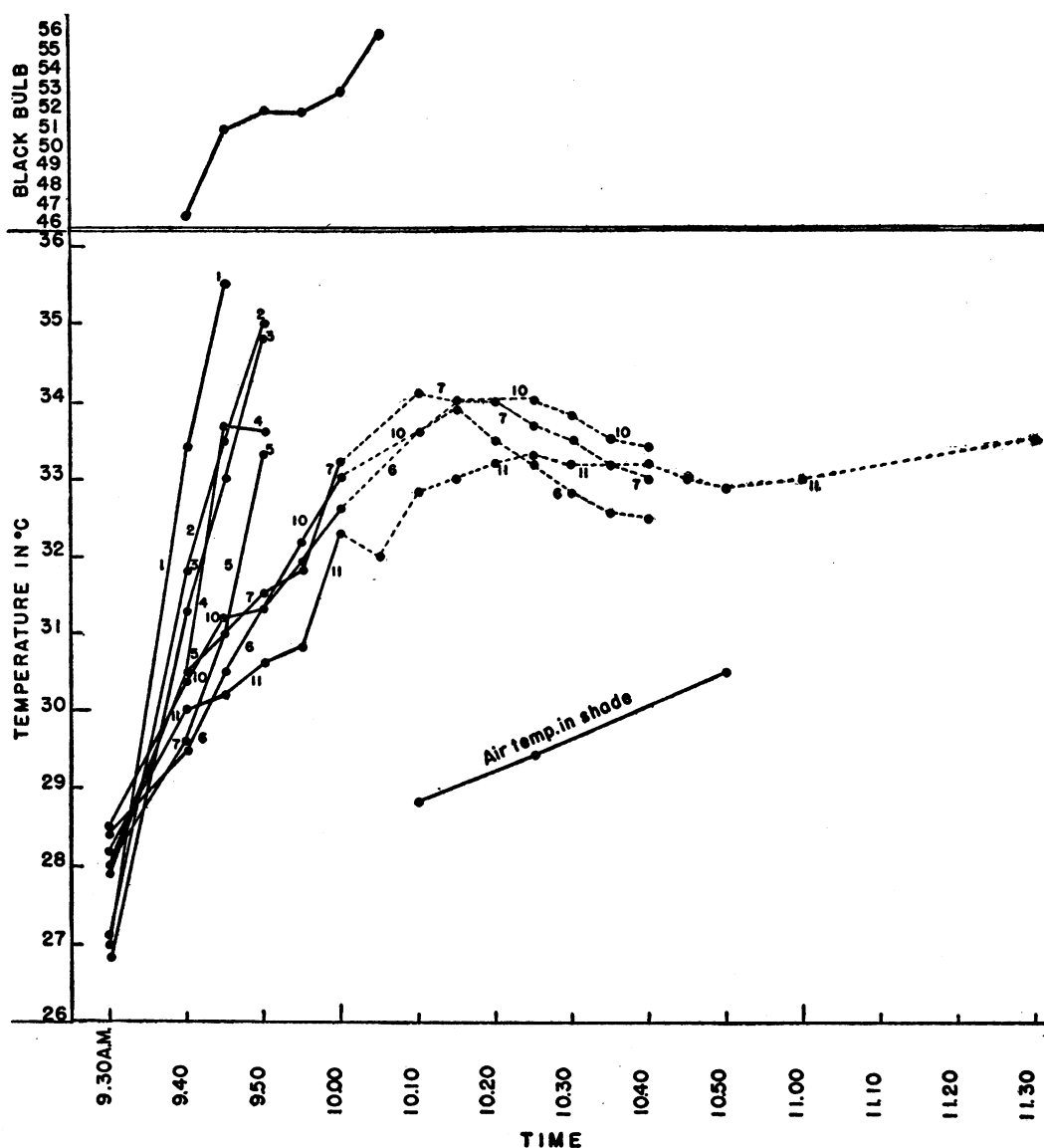


FIG. 4. Tolerance to heat in direct sunlight, showing rates of heat absorption and heat loss in alligators of various sizes. Second trial. Numbers indicate the animals used. The solid lines show temperature rises during exposure to the sun; the dotted lines show fluctuations of temperatures after the removal of the alligators to the shade. See table 5.

CONCLUSIONS

The results of this experiment were about what it was thought they would be before the experiment was made. That is, in direct sunlight the speed at which the temperature of the several alligators rose varied inversely with the size of the animals. It rose most rapidly in the smallest individuals, and most slowly in the largest individuals. This was a

simple function of the body mass involved in each case; in other words, the larger the mass of the animal, the longer it took for this animal to absorb heat throughout the extent of its body.

It was interesting to see, however, that although the small animals absorbed heat very rapidly, they also lost it rapidly. On the other hand, heat loss in the big animals was

very slow—indeed, there was even a rise in cloacal temperature after these large individuals had been removed from the sun to the shade.

From this experiment it is evident that there is much less sensitivity to minor or

intermittent temperature fluctuations (in this case, radiant heat) in the big reptiles than there is in the small ones—a point the importance of which will be discussed in a subsequent paragraph.

2. VOLUNTARY TOLERANCES

PURPOSE

In this experiment the purpose was to determine the temperatures that the alligators would tolerate when given a choice of being either in direct sunlight or in shade. Would the animals of smaller sizes prefer shade to direct sunlight? If so, at what body temperatures would the several individuals leave the sun for the protection of the shade? What would be the optimum temperature?

TECHNIQUE

A pen was made, the sides of which were lined with black paper. This was to prevent the slanting rays of the sun from entering the pen; also it provided shade on one or two sides of the pen. The center of the pen was exposed to the full rays of the sun. A few boards were placed over one end of the pen to provide additional shade. The substratum was of dark-colored pavement.

After initial temperatures had been taken the animals were placed in the middle of the pen, and their reactions were observed. Subsequent temperatures were taken for each individual, while shade temperatures and

black bulb readings were also recorded.

Two trials were made, one in the early afternoon when the sun was high, and one beginning in the very early morning just as the sun was coming up.

RESULTS

In both trials the animals remained in the shade and refused to go into the sunlight, except for short intervals when they were changing from one location to another. In the first trial, made in the afternoon, the animals were placed in the sun, and they all immediately sought the shade and stayed there. In the second trial the animals were placed in the pen before the sun came up, and as the sun rose they remained in the shade. This latter reaction was rather surprising for it had been supposed that they would seek the sun early in the morning for the purpose of basking.

In the shade the several individuals were able to regulate their temperatures by crowding against the black tar paper which lined the sides of the pen. That is, they could remain on the side of the pen away from the sun where the shade was relatively cool, or

TABLE 6
FIRST TRIAL

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators					
			No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
Sept. 6, 1944 Animals placed in open pen at 1:45 P.M.	1:45 P.M. (initial)		32.7° C. ^a	26.3° C. ^b	32.0° C. ^a	31.7° C. ^a	31.1° C. ^a	27.5° C. ^b
	2:00	60° C.	35.5	30.3	36.5	34.0	33.6	29.0
	3:00	47	32.5	35.2	35.0	34.6	32.5	34.0

^a Animal taken from sand at edge of pool.

^b Animal taken from pool.

they could rest against the paper on the sunny side to acquire heat that had been absorbed by the black paper from the direct rays of the sun.

It was interesting to see that the alligators preferred this latter position most of the time. Moreover, it was found that by doing this they were able to raise the body temperature to points between about 32° C. and 35° C., which seemed to be the preferred range. In other words, this range of approximately 32° to 35° C. represents an approximation of the

animals to attain temperatures beyond the desired upper limits. Given time, however, each individual was able to shift about and find the environment most suitable for itself.

Table 7 shows the adjustment of temperatures to the optimum range. In this case the temperatures attained occupied a narrower range than in the first trial, perhaps because the animals were less disturbed and were under more equable external temperature conditions.

TABLE 7
SECOND TRIAL

General Conditions	Time	Black Bulb	Air Temp.	Substr. Temp.	Cloacal Temperatures Alligators					
					No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
Sept. 7, 1944	Sunrise	—	25.0° C.	25.0° C.	26.0° C.	26.0° C.	26.0° C.	26.0° C.	26.0° C.	26.0° C.
At sunrise alligators all in water;	9:00 A.M.	38.5° C.	28.9	28.3	—	—	—	—	—	—
were shifted to	9:50	—	—	—	—	—	—	—	—	31.9*
open pen	11:00	53.5	33.5	33.0	33.5	33.2	34.5	34.3	34.2	34.5
Water temp., 26° C. Air temp., 25° C. Substratum temp., 25° C. These temps. probably approximated initial temps. of alligators										

* About 9:30, no. 6 came out into sun. Returned to shade at 9:50.

optimum basking temperatures. The results of the two trials, on animals nos. 1-6, are given in tables 6 and 7.

This trial (table 6) shows that animals of varying initial temperatures became adjusted in time to their optimum basking temperatures, namely, those temperatures in the range of 32° to 35° C. These temperatures were not quickly attained; indeed, it will be seen that the first effects were for the smaller

CONCLUSIONS

From this experiment it would appear that the preferred temperature in alligators out of the water is but a few degrees below the critical maximum. At this optimum range the metabolism of the individual is at a high and beneficial level, so that the animal enjoys a favorable relationship to its external environment.

3. TOLERANCE IN DINOSAUR POSTURES TO HEAT IN DIRECT SUNLIGHT

PURPOSE

Having determined the tolerance to heat in direct sunlight in a graded series of individuals, we made a test between individuals of the same size but posed in different manners. This was a test of the rate of heat absorption as related to posture.

The inspiration for this experiment came from a study of dinosaurian poses and habits. Generally speaking, there were two methods of progression among the dinosaurs, bipedal and quadrupedal. The bipedal method of locomotion was basic and primitive in these long-extinct reptiles, while the quadrupedal

method of progression was secondary. Naturally, during such times when the dinosaurs were not moving about, it is probable that they often would rest in a prone position, as do the recent crocodilians. What would be the rate of temperature rise in animals assuming these several postures, namely, that of bipedalism, that of quadrupedalism, and that of resting flat upon the ground? How did the habits and method of locomotion affect reactions to heat in the dinosaurs? Such were the questions that it was hoped might be solved, at least to some degree, by experiments with modern alligators.

TECHNIQUE

For this experiment it was necessary to have at least three alligators of as nearly the same size as possible. Therefore nos. 8, 9, and 10 were used, since these particular individuals were more or less alike as to body mass. As a matter of convenience the weights and measurements of these three individuals are repeated at this place.

SPECIMEN NO.	LENGTH	WEIGHT
8	1090 mm.	4772 gr.
9	1190	5681
10	1130	5909

The plan was to pose one of these animals in a manner similar to the posture assumed by the bipedal dinosaurs, that is, standing on the hind legs with the body at an angle of

about 40 degrees to the horizontal. Another animal was to be given the pose of a quadrupedal dinosaur, standing up on all four legs, with the belly well off the ground. The third animal was to be kept prone, with the belly flush with the ground, in the general pose assumed by recent crocodilians when resting or basking.

To maintain the animals in these poses three wooden frames were made, and the animals were lashed to the frames (see pl. 41, fig. 1). One frame was so constructed as to hold the animal on its hind legs, with the body at a 40-degree angle; another frame held the animal off the ground, but with the four feet resting on the surface in a walking pose, while the third frame merely held the animal flat on the ground.

After the animals had been securely fastened to the frames, in the shade, they were placed in the sun. The three animals were oriented with relation to the sun, in some cases facing the sun, and in other cases broadside to the sun. Some of the trials were made in the morning, with the sun at a moderately low angle; others, in the afternoon with the sun high. Also, some trials were made on the grass and others on pavement, so that a comparison between the two types of substratum might be obtained.

The purpose of orienting the animals with relation to the sun was to get a comparison between temperature or heat absorption in

TABLE 8
FIRST TRIAL

General Conditions	Time	Cloacal Temperatures Alligators			Notes
		No. 8 Quadrupedal Pose	No. 9 Bipedal Pose	No. 10 Flat on Ground	
Sept. 1, 1944					
Animals placed in sun at 9:10 A.M.	9:10 A.M.	27.0° C.	27.0° C.	27.0° C.	
Grass temp., 31.0° C.	9:25	29.2	28.8	28.7	
	9:40	30.8	29.0	31.1	
	9:55	33.2	30.6	33.2	
Air temp., 29.5° C. in shade	10:10	35.0	32.0	34.8	
Wind negligible	10:25	36.5	33.1	36.5	Trial concluded; clouds beginning to form

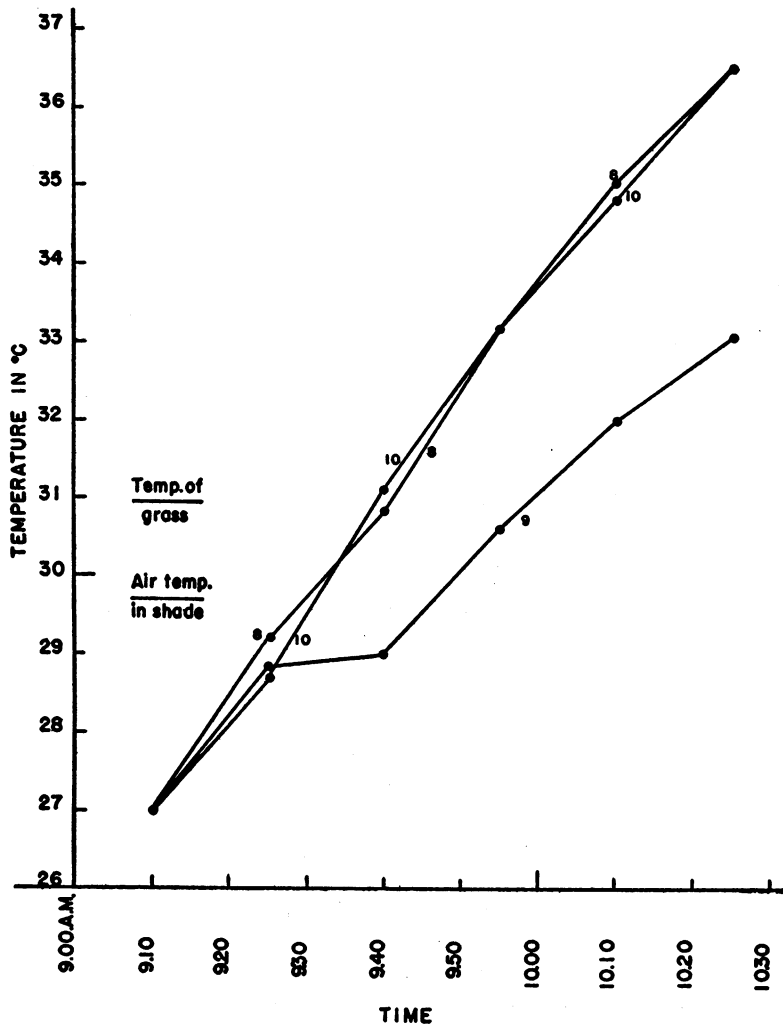


FIG. 5. Tolerance of alligators in dinosaur poses to heat in direct sunlight, showing rate of heat absorption as related to postures. First trial. Animal no. 8 in quadrupedal pose; no. 9 in bipedal pose; no. 10 flat on ground. See table 8.

poses whereby a minimum amount of body surface was exposed to the direct rays of the sun and in poses where a large or maximum amount of body surface was so exposed. Interesting results were obtained, and these are set forth below.

RESULTS

FIRST TRIAL

The first trial was made in the morning and on the grass. The animals were lashed to their respective frames, and initial temperatures were taken. They were then placed in the di-

rect rays of the sun, each animal facing it. Temperatures were taken at fifteen-minute intervals. Number 8 was placed horizontally with the belly off of the ground (as in a quadrupedal dinosaurian pose), no. 9 was placed at an angle (as in a bipedal dinosaurian pose), while no. 10 was placed flat on the ground.

It will be noted that whereas nos. 8 and 10 absorbed heat at approximately equal rates, the temperature of no. 9 rose more slowly. This is as might be expected, since in no. 9 there was less body surface exposed to the direct rays of the sun than in the case of the

TABLE 9
SECOND TRIAL

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators			Notes
			No. 8 Bipedal Pose	No. 9 Quad-rupedal Pose	No. 10 Flat on Ground	
Sept. 1, 1944 Animals placed in sun at 1:00 P.M.	1:00 P.M.	53.0° C.	29.5° C.	29.0° C.	30.3° C.	Substratum temp., 48.0° C. Thermometer placed on pavement, covered with sand swept from adjoining area
	1:05	53.0	30.2	29.5	31.0	
	1:10	56.0	30.8	31.0	32.4	
	1:15	55.5	32.0	32.0	33.6	
	1:20	56.0	32.9	33.0	34.9	Light clouds
	1:25	56.5	33.0	33.9	36.0	Sunny
	1:30	57.0	33.9	34.6	—	No. 10 removed to shade
	1:35	53.0	34.8	35.4	—	Clouds
	1:40	49.0	35.7	36.2	—	Clouds
						Trial concluded

TABLE 10
THIRD TRIAL

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators			Notes
			No. 8 Bipedal Pose	No. 9 Quad-rupedal Pose	No. 10 Flat on Ground	
Sept. 2, 1944 Animals placed in sun at 8:45 A.M.	8:45 A.M.	—	27.2° C.	27.0° C.	27.5° C.	
	8:55	48.0° C.	28.4	27.8	28.7	No. 8 belly exposed to slanting rays of sun
	9:05	51.0	29.0	28.5	29.6	
	9:15	53.0	30.0	29.5	31.2	
	9:25	54.0	30.8	30.6	31.5	
	9:35	56.0	31.6	31.6	33.5	
	9:45	54.0	32.5	32.9	34.2	No. 8 belly partially shaded No. 10 removed to shade
	9:55	57.0	33.0	33.3	36.0	
	10:05	47.0	34.0	35.1	—	
	10:15	42.0	34.2	35.1	—	No. 8 belly completely shaded No. 9 removed to shade
	10:25	52.0	34.6	36.0	—	
	10:35	61.0	35.4	—	—	No. 8 removed to shade
	10:45	61.0	36.0	—	—	

two horizontally placed alligators. The fact that the temperature of no. 10 rose no more rapidly than no. 8 is somewhat astonishing, since in the latter animal the body was off the ground, so that there was circulation of air

underneath the body with consequent cooling effects. It is probable, however, that the temperature of no. 10 was held down by contact of the entire ventral surface with the comparatively cool and damp grass.

SECOND TRIAL

The second trial was made in the afternoon, and on the pavement, which consisted of crushed limestone set in asphalt so that the surface was very rough. The animals were not enclosed in any way, but there was no appreciable wind. Thus there was considerable contrast between the conditions under which this trial was made and those holding for the previous trial. The alligators were placed in the sun at 1:00 P.M., and temperatures were taken at five-minute intervals. In this trial no. 8 was placed at an angle (bipedal pose), and no. 10 was placed flat upon the ground, as before. All animals were faced toward the sun.

In the second trial (table 9) the contrast between the two raised animals and the prone animal was marked. It would seem evident that the relatively rapid rise in temperature of no. 10 was due to a considerable extent to the fact that this animal was absorbing heat from the substratum, as well as from the direct rays of the sun. Also, because of the pose there was no ventilation on the ventral surface of this animal as was the case with the animals raised on frames. The under surface of the belly and tail were flat on the pavement, but the head was raised. It will be noticed that the temperature rises in the two other animals were closely parallel; here we see the effect of a high sun, as contrasted with the low morning sun, so that the difference in posture in these two animals had little effect on their respective rates of heat absorption. Thus, although both animals were oriented with their heads toward the sun, both received the direct rays of the sun on their backs, whereas in the previous trial, performed in the morning, the animal in the bipedal pose received very little sunlight either on the back or upon the ventral surface.

THIRD TRIAL

The third trial was made in the morning, as in the case of the first trial, but this time it was made upon the pavement described above. The alligators were placed in the sun at 8:45 A.M., and temperatures were taken at ten-minute intervals. The poses were the same as in the second trial, no. 8 being placed in a bipedal pose, no. 9 in a quadrupedal pose,

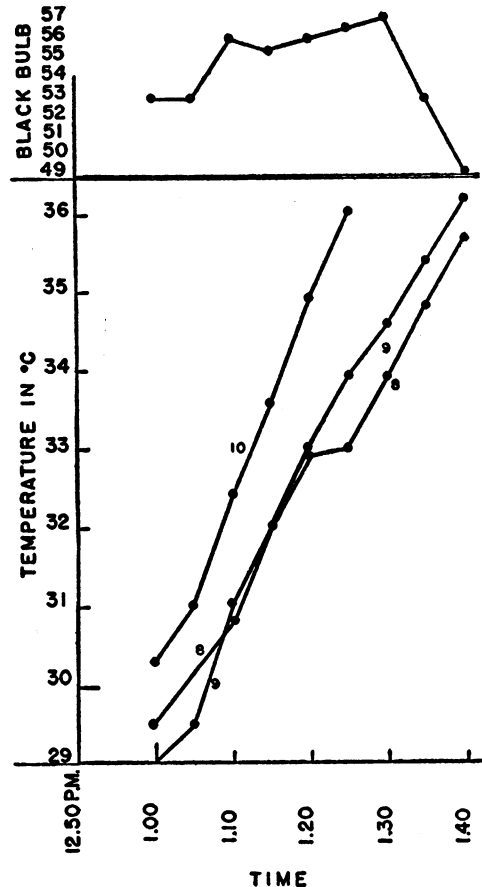


FIG. 6. Tolerance of alligators in dinosaur poses to heat in direct sunlight, showing rate of heat absorption as related to postures. Second trial. Animal no. 8 in bipedal pose; no. 9 in quadrupedal pose; no. 10 flat on ground. See table 9.

and no. 10 flat upon the substratum. As in the previous trials, the animals were all placed facing the sun. There were light, intermittent clouds during the latter part of the experiment, but they did not seem to effect materially the results of the experiment.

The results of the third trial confirm the evidence afforded by the first trial. It is clear that with the animals facing the slanting rays of the sun, posture does affect the internal temperature control. The animal standing in a bipedal pose received the least amount of direct sunlight upon the body, and such rays as did strike the belly or the back met the surface of the body at a low angle. Therefore the temperature of this animal rose much more slowly than did the temperatures of the

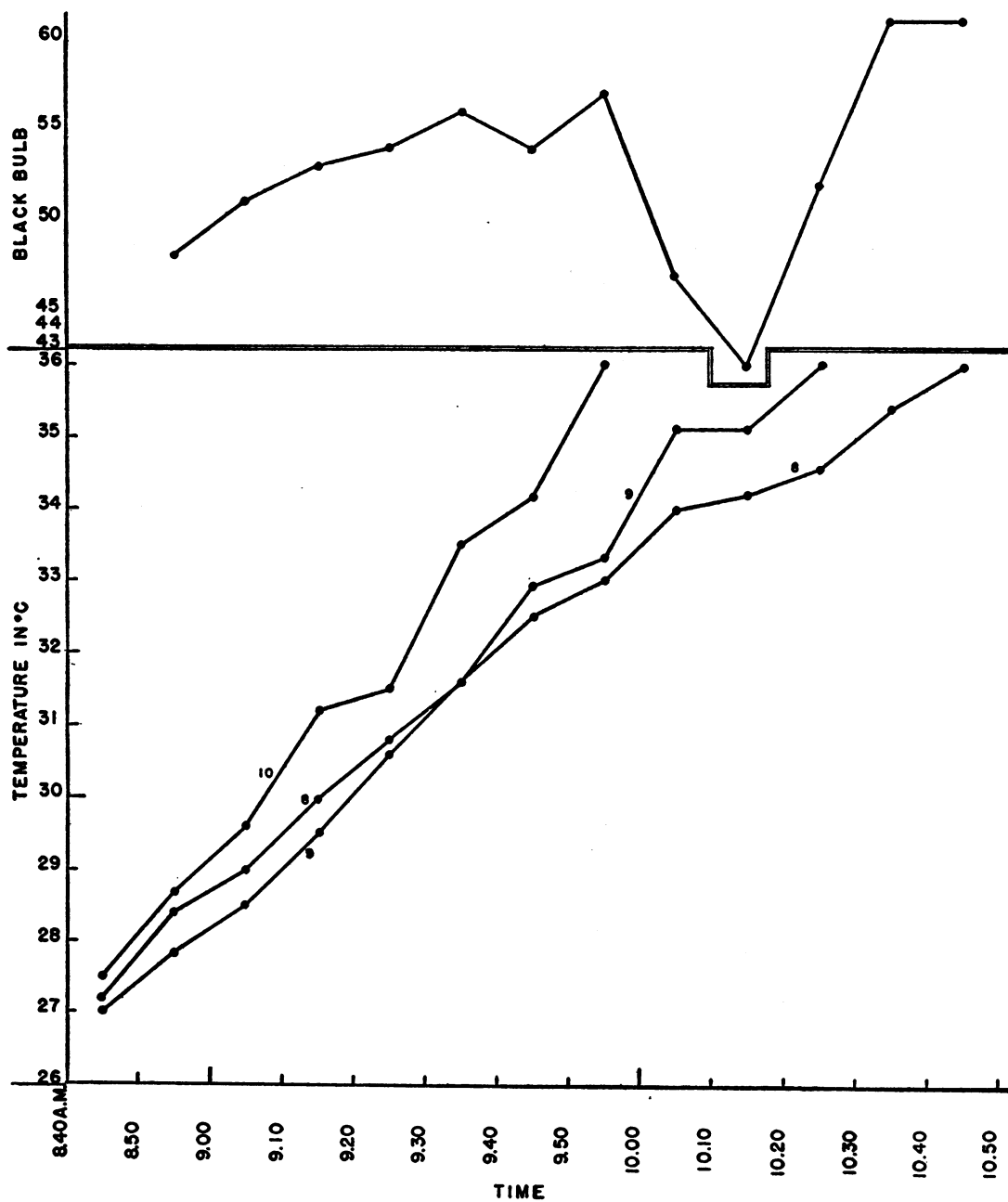


FIG. 7. Tolerance of alligators in dinosaur poses to heat in direct sunlight, showing rate of heat absorption as related to postures. Third trial. Animal no. 8 in bipedal pose; no. 9 in quadrupedal pose; no. 10 flat on ground. See table 10.

TABLE 11
FOURTH TRIAL

General Conditions	Time	Black Bulb	Cloacal Temperatures Alligators			Notes
			No. 8 Bipedal Pose	No. 9 Quad-rupedal Pose	No. 10 Flat on Ground	
Sept. 6, 1944 Animals placed in sun at 9:45 P.M.	9:45 A.M.	—	28.2° C.	28.1° C.	28.2° C.	
	9:50	47.5° C.	28.6	29.0	29.2	
	9:55	49.0	29.5	30.0	31.0	
	10:00	47.0	30.5	30.5	31.5	
	10:05	50.0	31.0	31.0	32.0	
	10:10	52.0	32.0	32.1	32.0	
	10:15	48.0	33.0	33.1	34.0	Very light clouds
	10:20	47.0	33.1	34.0	34.0	
	10:25	53.0	34.2	34.2	35.2	Trial ended

other two animals. It is interesting to see that in this trial, as in the preceding trial, the prone animal evidently absorbed an appreciable amount of heat from the substratum.

Another point to be brought out in connection with this trial is the fact that, although during a part of the trial the sun was obscured by clouds, the cloacal temperatures of the alligators continued to rise. Here we see the cumulative effect of heat absorption in reptiles of considerable size.

Toward the end of the trial, no. 9 obviously was rather weak. Here again it would seem that cumulative effects of heat absorption were being felt, as a result of the three trials made within a period of slightly more than 24 hours. Because of this, further trials were postponed to a later date.

FOURTH TRIAL

The fourth trial was made in the morning so that the slanting rays of the sun might be utilized, but in contradistinction to the previous trials, the animals were placed at *right angles* to the sun. The trial was made on the grass, and the animals were placed in the sun at 9:45. Temperatures were taken at five-minute intervals. Number 8 was given a bipedal pose, no. 9 a quadrupedal pose, and no. 10 was placed flat on the ground. The results of the trial are given in table 11.

In contrast with the other trials, the fourth trial was marked by the close parallelism of temperature rises in all the animals. Here we see the results of the various individuals getting approximately the same effects from the sunlight, in spite of their different poses. That is, the three individuals, being at right angles to the sun, were affected about equally by the sunlight. Since the experiment was made on the grass, the absorption of heat from the substratum in the case of no. 10 was to a large degree probably held down to a minimum.

CONCLUSIONS

From this experiment it has been shown that a certain degree of temperature control, depending upon varying postures, is manifest among reptiles of considerable size. When alligators are placed facing the sun their temperatures rise at different rates, depending upon the postures assumed by the animals. An alligator in a bipedal posture shows the slowest rate of temperature rise, while the animal flat on the ground generally shows the highest rate of such rise. The animal in a quadrupedal pose is generally intermediate with regard to the rate of temperature increase.

These differences are due to a number of factors. In the animals assuming bipedal and

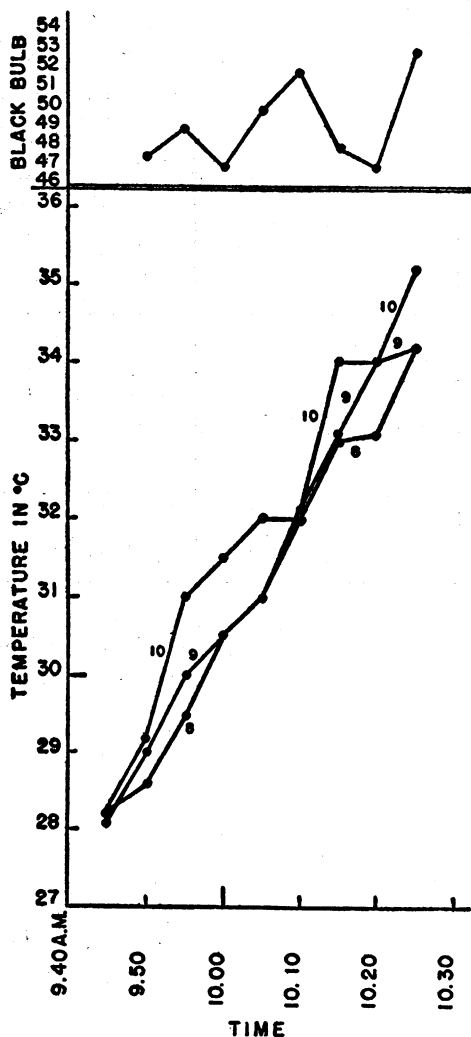


FIG. 8. Tolerance of alligators in dinosaur poses to heat in direct sunlight, showing rate of heat absorption as related to postures. Fourth trial. Animal no. 8 in bipedal pose; no. 9 in quadrupedal pose; no. 10 flat on ground. See table 11.

4. TOLERANCE TO CONSTANT TEMPERATURES NEAR THE CRITICAL MAXIMUM

PURPOSE

The purpose of this experiment was to determine the response of an alligator to a constant temperature, under conditions of constant humidity. How would the animal react to a high temperature? Would it be able to

quadrupedal poses there is free circulation of air, with a consequent cooling effect beneath the body, while on the other hand the animal prone upon the ground absorbs heat (or loses it, of course, if the ground is colder) from the substratum. Moreover, the animal in a bipedal pose exposes less body surface to the rays of the sun, when it faces the sun, than does the animal in a quadrupedal pose or the animal flat upon the ground; therefore the temperature rise of the former is slower than that of the latter two. As Cowles and Bogert have shown (1944, pp. 289-290) this same end is accomplished among modern desert lizards during the hot part of the day, when they face the sun and raise the forequarters as high off the ground as possible by straightening the front legs.

All of this suggests that among the dinosaurs of Mesozoic times there may have been a certain amount of temperature control depending upon posture. The various bipedal dinosaurs, by facing the sun, might have held down the rate of heat absorption. The quadrupedal forms might have been more adversely affected by heat than the bipedal dinosaurs, but even so, they probably were less subjected to rapid temperature rises than were contemporary crocodilians which when on land presumably rested with their bellies flush with the ground.

survive, by making physiological adjustments to the conditions under which it was being tested?

TECHNIQUE

In this experiment the animal was sub-



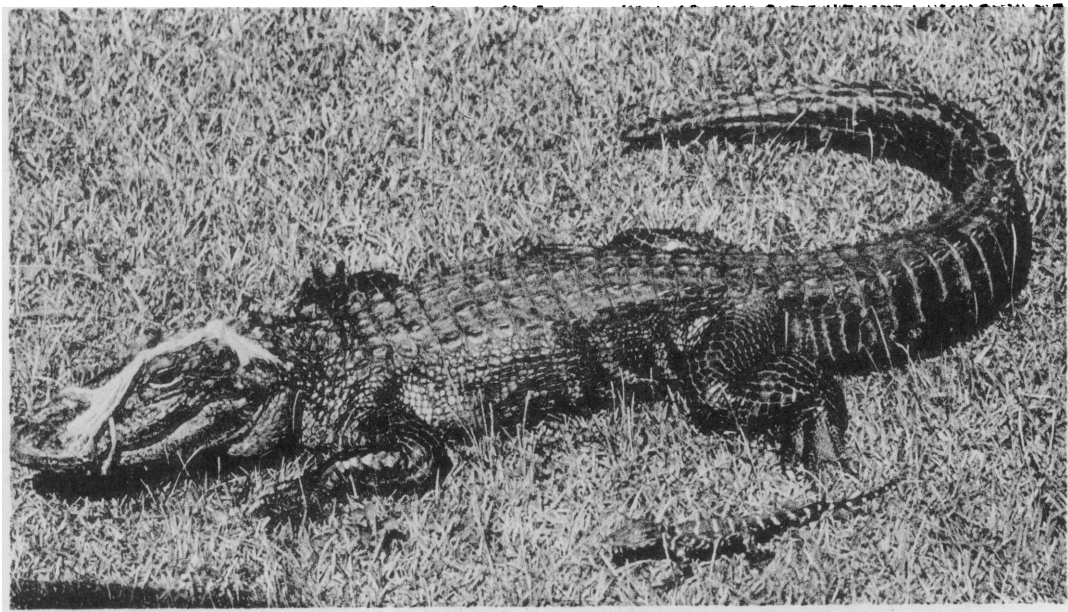
1. One branch of Fisheating Creek about 15 miles south of the Archbold Biological Station, in Glades County, Florida. Alligators were observed here, in water with temperatures of 26° C. at the surface



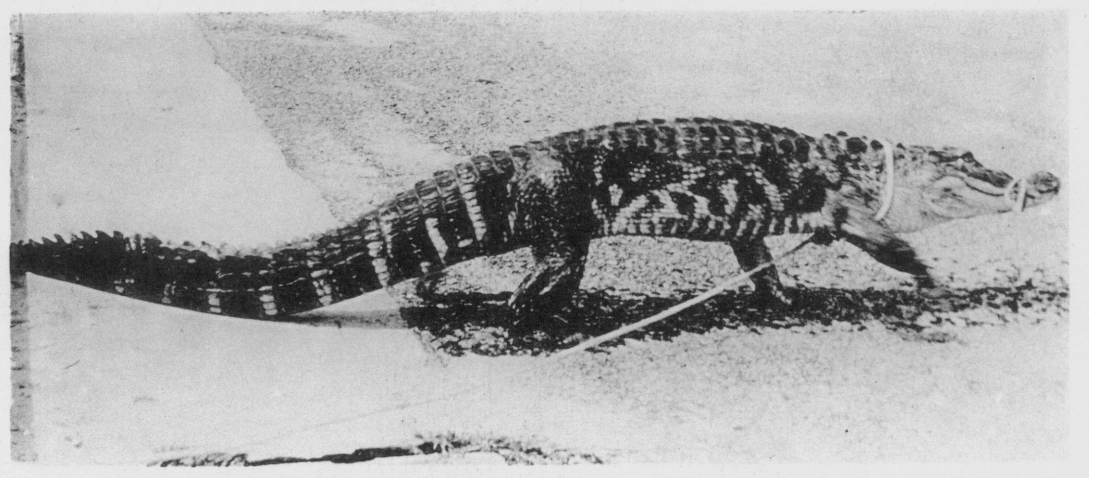
2. A small pool with surface temperature of 31° C. on the grounds of the Archbold Biological Station, in southern Highlands County, Florida. A three-foot alligator inhabited this pool



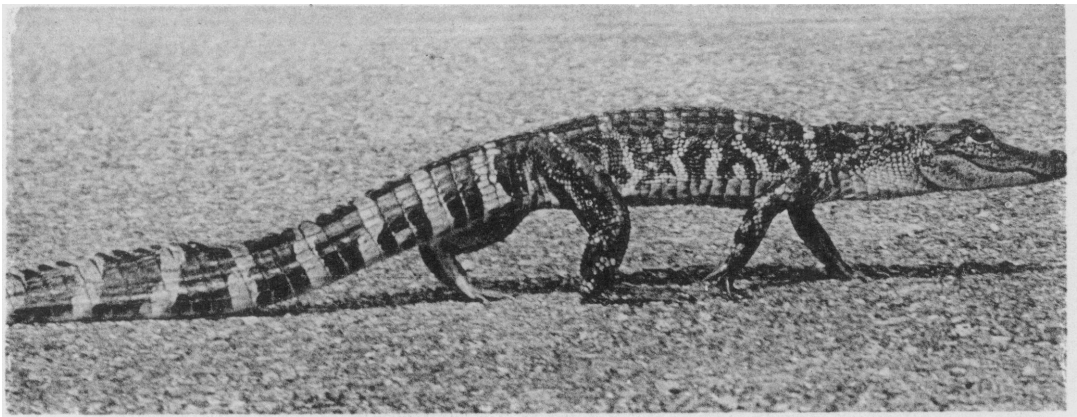
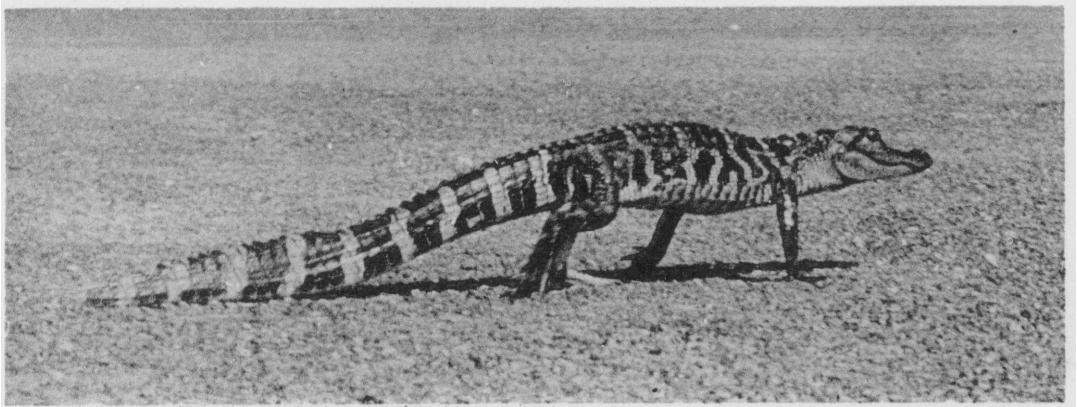
1. The largest alligator (No. 12) used in the experiments, with an over-all length of 1981 mm. (78 inches) and a weight of 24,501 grams (54 pounds)



2. The next to largest (No. 11) and the smallest (No. 1) alligators used in the experiments. The over-all length and weight of No. 11 were 1510 mm. and 13,068 grams, respectively; of No. 1, 275 mm. (11 inches) and 47.5 grams (1.7 ounces)



1. Posture while walking of alligator No. 12, with the belly raised off the ground



2, 3. Posture of alligator No. 13, a smaller individual, while walking. These pictures show clearly the elevated position of the body in alligators, at speeds not exceeding 1 mile an hour



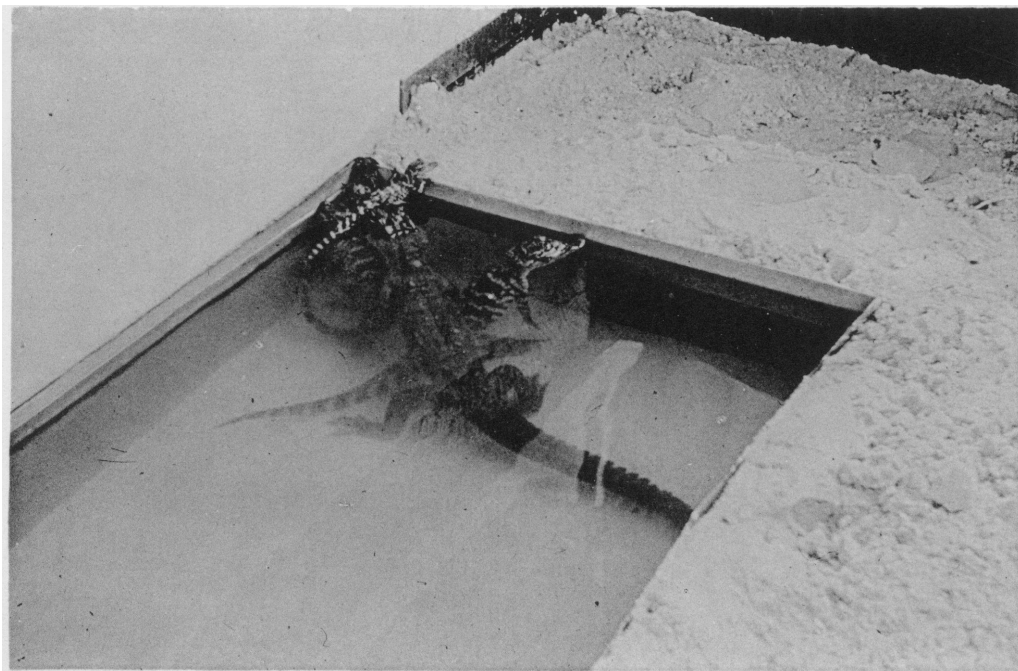
1. Method of taking cloacal temperatures during experiments



2. Alligators of a series graded in size, tied to stakes on a lawn, during experiment dealing with tolerance to heat in direct sunlight



1. Pool in enclosure constructed for experiments dealing with tolerances to hot and cold water



2. Alligators prior to emergence from the pool as the temperature of the water approached the maximum tolerated. Note smallest alligator in the series about to come out of the water



1. Three alligators of approximately similar sizes tied to frames, in order to simulate dinosaurian poses. (a) Quadrupedal, with the belly raised off the ground. (b) Bipedal, with the main axis of the body at an angle of 40 degrees. (c) Prone or resting posture, with belly flush with the ground



2. Scene along the Caloosahatchee River in southern Glades County, Florida. Water at the surface here approximated 37°C . No alligators were observed in water at this high temperature. At Silver Springs, in Marion County, Florida, alligators inhabit water with a constant temperature slightly exceeding 23°C .

TABLE 12

FIRST TRIAL

General Conditions	Date	Time	Alligator No. 5 Cloacal Temperatures	Weight	Notes
Temp. in chamber, 38.0° C. Relative humidity, 37%	June 6, 1944	2:30 P.M.	27.0° C.	668.1 gr.	Initial temp. and wt.
		2:45	33.5		
		3:00	35.5		
		3:15	36.5		
		3:30	36.8	652.7	Voided water
		3:50	37.2		Very active
		4:15	37.4		
		4:30	37.5		
		5:00	37.0	644.4	
		5:30	37.5		
		6:00	37.5		
		7:00	38.0		
		9:30	37.4		
		11:00	37.5	612.4	
	June 7, 1944	1:00 A.M.	37.5		
		7:45	37.5	568.0	
		11:00	37.5		
		1:30 P.M.	37.6		
		2:30	37.4	534.6	Removed in good condition

jected to an environment that was admittedly artificial. It was placed in a constant temperature-humidity chamber, in which conditions could be rigidly controlled. Temperature fluctuations were no more than 0.4° C. in the chamber, and the humidity was nearly constant in each trial. Thus the temperature and humidity of the chamber were set and determined before the animal was placed in the chamber. The animal was placed in a small, wire mesh cage already in the chamber, in which it remained quiescent during the experiment.

RESULTS

FIRST TRIAL

From the data presented in table 12, it is apparent that during the twenty-four-hour period that the alligator was in the constant temperature-humidity chamber it lost 133.5 grams, or approximately 20 per cent of its total initial body weight. After the animal was removed from the chamber it was placed

in water at 27° C., and rapidly gained weight by the absorption of water. The data are given in table 13.

SECOND TRIAL

The second trial was made three months after the first trial, but with the same animal. In the intervening time the alligator had lost a little weight, and presumably may not have been in quite so good condition as it was at the time the first trial was made. However, the difference was small. This trial was run for 12 hours, as compared with the 24 hours for the first trial.

In the second trial of this experiment, we see a loss of weight by the alligator in the chamber, but rather less than in the first trial. Thus in this trial the loss of weight over a twelve-hour period is approximately 6.5 per cent, which may be compared with the 10 per cent loss over a similar period of time in the first trial when the relative humidity was somewhat less.

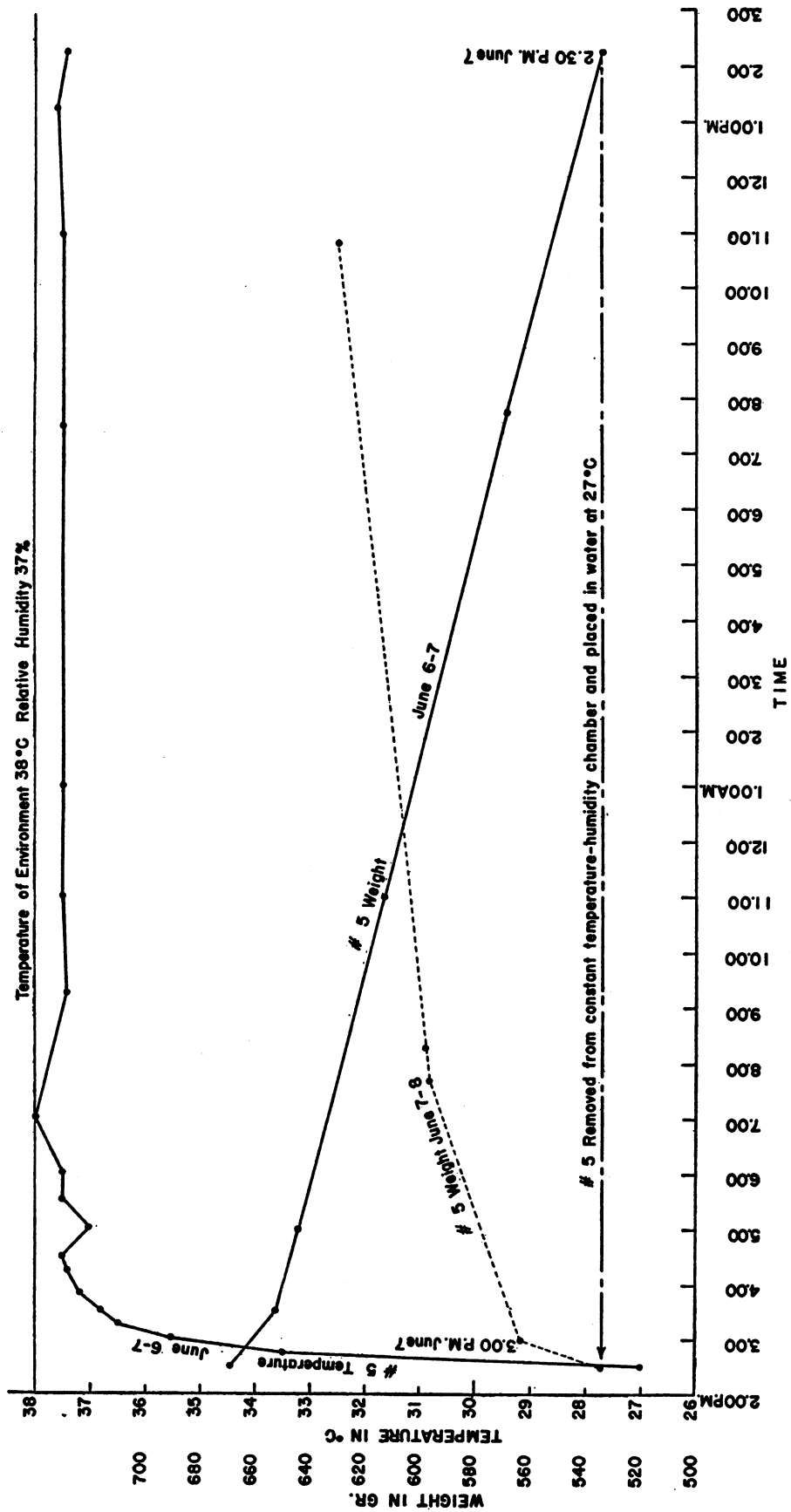


FIG. 9. Tolerance of alligator no. 5 to constant temperatures near the critical maximum. First trial. Solid line indicates rate of moisture loss in the thermal chamber. Dotted line shows the recovery of moisture of the animal when removed and placed in water. See table 12.

TABLE 13
ALLIGATOR No. 5

General Conditions	Date	Time	Weight
Placed in water at 27° C.	June 7, 1944	3:00 P.M.	563.3 gr.
		7:40	595.3
	June 8, 1944	10:50 A.M.	629.6

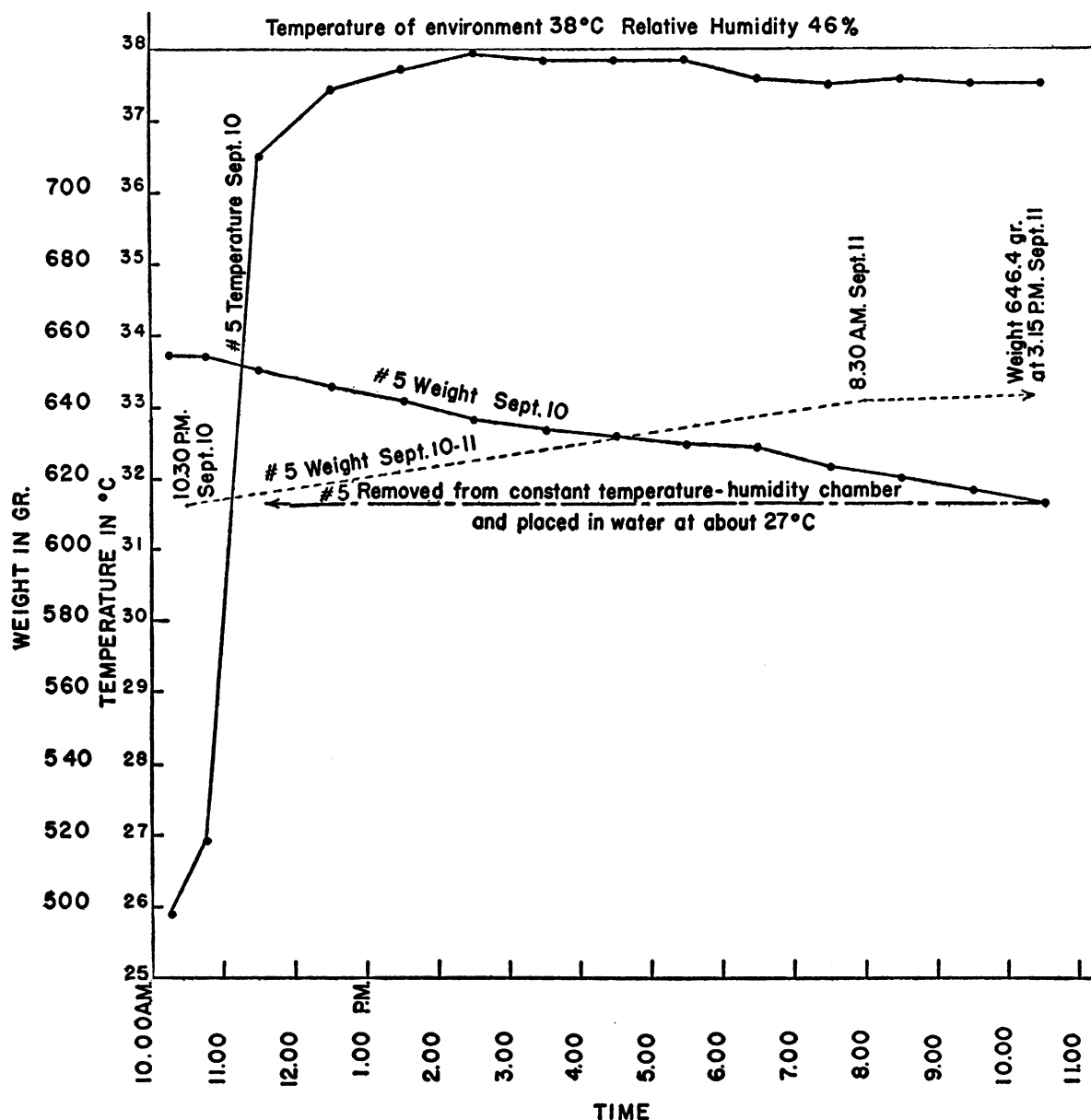


FIG. 10. Tolerance of alligator no. 5 to constant temperatures near the critical maximum. Second trial. Solid line indicates rate of moisture loss in the thermal chamber. Dotted line shows the recovery of moisture of the animal when removed and placed in water. See table 14.

TABLE 14
SECOND TRIAL

General Conditions	Time	Alligator No. 5		Notes
		Cloacal Temperatures	Weight	
Sept. 10, 1944 Temp. in chamber, 38.0° C. Relative humidity, 46%	10:15 A.M.	25.9° C.	654.5 gr.	Initial temp. and wt.
	10:45	26.9	654.5	
	11:30	36.5	650.3	
	12:30 P.M.	37.4	645.2	
	1:30	37.7	641.8	
	2:30	37.9	636.3	
	3:30	37.8	634.2	
	4:30	37.8	632.0	
	5:30	37.8	629.9	
	6:30	37.6	628.3	
	7:30	37.5	623.0	Defecated
	8:30	37.6	620.0	
	9:30	37.5	617.0	
	10:30	37.5	613.2	Removed

CONCLUSIONS

This experiment shows that the alligator may survive environmental temperatures approximating the critical maximum for a comparatively long period of time, provided it is able to control its body temperature by a rapid and a relatively large loss of water through evaporation. It is interesting to see how the temperature of the animal in each trial quickly went up to a point but slightly under the critical maximum of approximately 38° C., and remained fairly constantly at this high point with very little apparent deleterious effects upon the animal. It is also interesting to see how much body water was lost during the process. Obviously there would have been definite limits to the length of time that any animal could withstand this treatment. Hall (1922, p. 45) states that some lizards "were exsiccated to . . . 47.8% of their body weight . . . before death occurred."

It will be noted that the loss of weight was somewhat greater in the first trial than in the second trial. Perhaps this was due to the fact that relative humidity was some nine points

lower in the first trial, thereby affording greater opportunity for rapid evaporation than was the case in the second trial. Also it may be noted that the animal's temperatures were slightly higher in the latter trial. From the previous experiments made out of doors it is evident that when the humidity is high these animals are more adversely affected by high temperatures than is the case when the humidity is relatively low, because in the case of high humidity the animal is correspondingly less able to make physiological adjustments to unfavorable temperature by evaporation of the body fluids than is the case when the humidity is low.

This experiment suggests the possibility that in the recent crocodilians and, by inference, in the long-extinct dinosaurs, there is and was a certain amount of adjustment to unfavorably high temperatures by evaporation. However, since these animals live now, and have generally lived in the past, in subtropical or tropical climates where high humidity is the rule, it is probable that such a method of temperature control is and has been of relatively minor importance.

5. TOLERANCE TO HOT WATER

PURPOSE

This experiment was an extension, by a different technique, of the attempts already made in previous experiments to determine tolerances of alligators to heat. In the first experiment alligators of different sizes were subjected to direct sunlight in order to determine the limits of their temperature tolerances, while in the second experiment an effort was made to determine their voluntary tolerances, or rather their preferences, to the heat of the sun. The experiment now to be described combined certain features of both the first and second experiments, in that it subjected the animals to a constantly increasing temperature as in the first experiment, but allowed them to make a voluntary adjustment to this temperature as in the second experiment.

How would alligators of varying sizes react to a constantly increasing temperature? It is to be supposed that the smallest individuals would be the first to feel the rise in temperature. Would they therefore be the first to react to such a rise? Given the opportunity of voluntary adjustment to ever increasing heat, would the animals withstand this heat until they had reached a point near the critical maximum, or would they seek relief at a much lower temperature? Would the animals prefer to undergo unfavorable temperatures in an environment which to them seemed "secure" rather than to seek relief from high temperatures in "less secure" surroundings?

TECHNIQUE

A large metal tank was constructed, 193 cm. in length by 71 cm. in width and 26 cm. in depth, and placed out of doors. Arrangements were made so that after the tank had been filled with water at air temperature, which was approximately 26° C., hot water could be run in at one end, forcing the cooler water out at the other end of the tank. In this way the water in the tank could be gradually heated to points necessarily high for the proper procedure of this experiment. At first an attempt was made to heat the water by means of an electric coil, but this proved much less satisfactory than the method of running hot water into the tank to displace the water at a temperature of 26° C. This also prevented much stratification of heat in the tank.

The alligators were placed in the tank and allowed to become accustomed to it. Then the water was gradually heated, by the method described above, and a careful watch was maintained to see the order in which the animals left the water. As each animal came out of the tank onto dry land it was caught and the cloacal temperature was taken. During this experiment the observers were careful to stay out of sight of the alligators as much as possible, so that the animals would not be prevented from leaving the water because of fear. In some trials of this experiment the tank was completely open on top, while in one trial one end of the tank was covered, to

TABLE 15
FIRST TRIAL

General Conditions	Order of Emergence	Alligator No.	Cloacal Temperatures
Aug. 30, 1944, afternoon	1	1	39.0° C.
Tank open at top; lined with black paper	2	2	39.0
Alligators nos. 1-6 incl. in tank	3	3	39.5
Initial water temp., 27° C.	4	4 } came out	38.5
Water raised within 30 min. to 42.0° C.	5	5 } together	36.5
	6	6	35.0

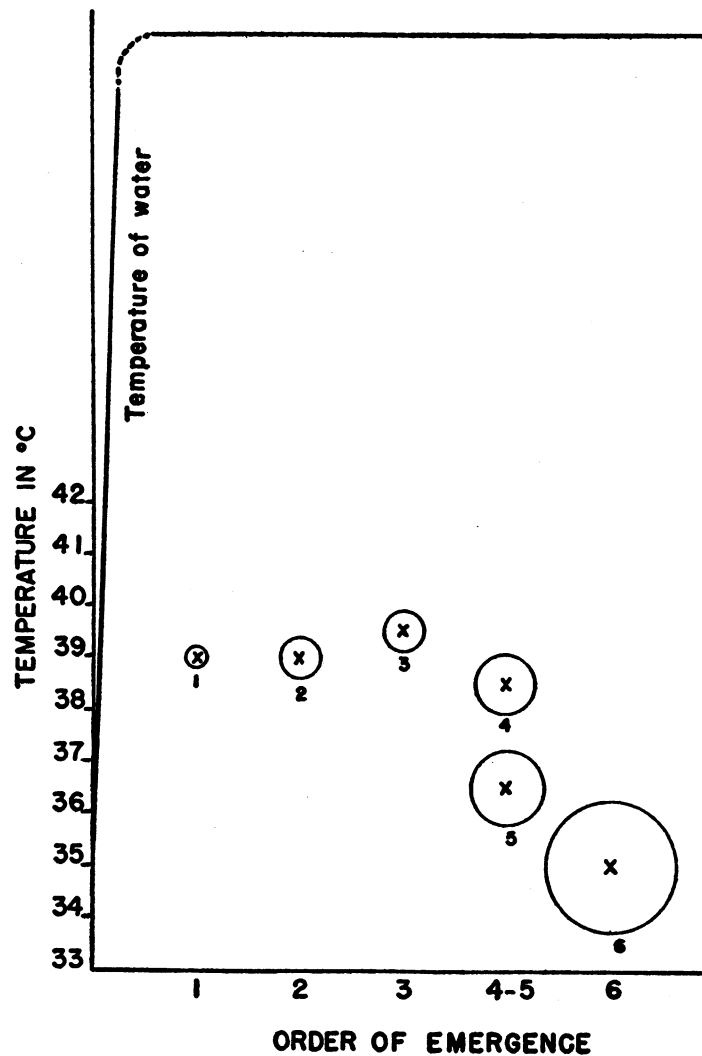


FIG. 11. Tolerance to hot water, showing correlation between order of emergence and body weights. First trial. Size of circles proportional to body mass; numbers indicate the animals used. See table 15.

make a dark "haven" for the alligators. A constant check was made on the temperature of the water in the tank.

The six smaller animals of the series, nos. 1 to 6 inclusive, were used for this experiment. The larger animals were not used because of the limitations of space imposed by the size of the tank. It was noticed that, generally speaking, when the trials were not being run, the alligators preferred to stay in the water most of the time. This was regarded as

a factor favorable to the proper conducting of the experiment. The animals felt secure in the water—at least more secure and more comfortable than they did on land. This feeling of security evidently was increased in the trial in which a cover was provided at one end of the tank. Consequently the alligators would be prone to stay in the tank as long as possible, and for this reason their greatest possible voluntary tolerance to heat would be approximately determined. Three trials were

TABLE 16
SECOND TRIAL

General Conditions	Alligator No.	Cloacal Temperatures	Notes
Aug. 31, 1944, morning	1	36.5° C.	Alligators refused to come out of "haven," even after prolonged exposure (over 1 hr.) to temps. slightly below critical maximum Animals removed, one by one, and temps. taken
Tank covered at one end, lined with black paper to make a dark "haven"	2	36.0	
Alligators nos. 1-6 incl. in tank	3	36.0	
Initial water temp., 26.5° C.	4	36.0	
Water temp. raised slowly to 36°-37° C.	5	36.0	
	6	36.0	

made, the results of which are presented in tables 15, 16, and 17.

The reader is referred to page 335 for a record of the lengths and weights of the animals used in this experiment.

RESULTS

FIRST TRIAL

As the water became hot the alligators showed obvious signs of discomfort and stayed at the bottom of the tank where the temperature was lowest. It is interesting to see how the order of emergence from the tank was in almost exact accord with the size of the animals concerned. The smallest alligator was forced to leave first because it absorbed heat most rapidly, while the largest animal, absorbing heat at the slowest rate because of its comparatively great bulk, was able to remain in the tank for the longest time.

One astonishing fact was the high temperatures attained by the three smallest animals. As shown by previous experiments in the sun (see tables 2 and 3), small alligators are able to attain temperatures even beyond the average critical maximum for larger specimens and to survive if these temperatures are not held for more than a few minutes at a time.

When the water had gone down to a temperature of 35.4° C., three of the alligators voluntarily went back into the pool. These were nos. 6, 2, and 4.

Later, when cold water was being run into the tank, all the animals flocked to the cold water inlet. After testing this reaction it was concluded that the animals had gathered because of the cooler water temperature at that end of the tank, rather than because of the current.

TABLE 17
THIRD TRIAL

General Conditions	Order of Emergence	Time	Alligator No.	Cloacal Temperatures	Notes
Aug. 31, 1944, afternoon	1	1:55 P.M.	1	35.0° C.	Replaced in tank
Tank open and without lining; bright reflecting inner surface	2	2:00	5	34.7	Replaced in tank
Alligators nos. 1-6 incl. in tank	3	2:05	1	36.0	Replaced in tank
Initial water temp., 30.0° C.					
Water slowly brought to equilibrium at 36°-37° C. (37° at surface, 36° at bottom of tank)					

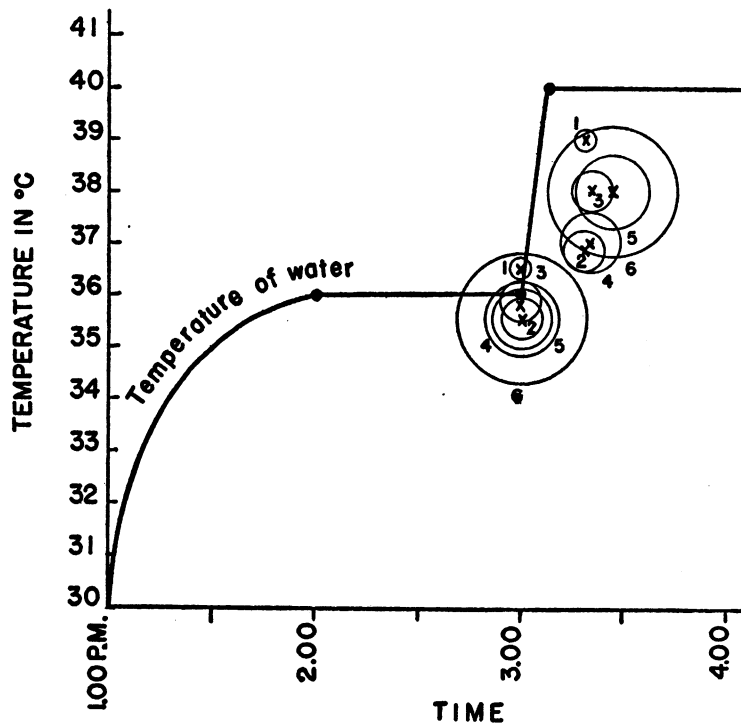


FIG. 12. Tolerance to hot water, showing correlation between order of emergence and body weights. Third trial. Size of circles proportional to body mass; numbers indicate the animals used. See tables 16-19.

SECOND TRIAL

Arrangements were made, in carrying out the second trial, to heat the water more slowly, in order to give the alligators sufficient time to adjust their body temperatures to the rising water temperature during the progress of the experiment.

Obviously the temperatures of the alligators were virtually identical with the temperature of the water. Otherwise the results of the second trial were not conclusive. What they did show was that the alligators were willing to withstand temperatures definitely unfavorable to them, rather than to come out of the security of their dark retreat. It is probable that if the temperature of the water had been raised still higher the animals would have been forced out of their haven, but it was felt that such a procedure was not worth the risk of possibly injuring or killing any of these alligators, thereby breaking the graded series available for further experiments.

THIRD TRIAL

The previous trials of this experiment showed that a dark retreat has a great influence on the behavior of alligators, an influence so strong that temperatures decidedly unfavorable are tolerated by individual animals before they forsake it. Therefore it was decided to try the experiment in an open tank, without any black lining. This would make the tank seem less like a safe refuge to the alligators, especially since the tank was painted with aluminum paint and consequently had a high light-reflecting value.

The water was maintained at an equilibrium of approximately 36° C. for some time, and the alligators refused to leave the tank. At 3:00 P.M. the animals were removed one by one, their temperatures were taken, and they were then replaced in the tank.

It is evident from table 18 that the alligators had reached a temperature virtually identical with that of their environment by

TABLE 18

ALLIGATOR No.	TEMPERA- TURE	NOTES
1	36.5° C.	Temps. of alligators at 3:00 P.M. after remaining for considerable time in tank, with the water temp., 36° C., except at surface
2	35.5	
3	35.8	
4	35.5	
5	35.5	
6	35.5	

3:00 P.M. It is interesting to note that the smallest animal, which habitually floated on the surface of the water and was thus subjected to the surface temperature, had a slightly higher temperature than the other animals, which were able to remain on the bottom of the tank.

After the alligators were put back in the tank at temperatures approximately the same as that of the water, hot water was quickly run into the tank so that the water temperature was raised to 39°–40° C. The animals quickly left the tank as shown in table 19.

It will be seen in table 19 that the animals came out in an order approximating their size. Since nos. 1 and 2 came out almost si-

multaneously, the only real departure from size in order of emergence was the reversal of nos. 3 and 4. Number 4, which came out first, had a lower temperature than no. 3 which followed it. Here once again we see the ability of the small alligator, no. 1, to withstand temperatures above the general critical maximum temperature, and once again we see the reluctance of the other animals to leave the water, even under conditions of very unfavorable temperatures.

CONCLUSIONS

By methods different from those used before, it has been shown that the rate of rise in body temperature in the alligator is in inverse order to the body mass. Also we see from this experiment that alligators will undergo unfavorable temperatures, almost to the point of attaining their critical maximum, rather than leave the water, where they feel safer than they do on land. It is a demonstration of the essentially aquatic nature of these beasts. Crocodilians presumably resort to water to escape heat under normal conditions, and in natural pools the depths would be cooler than the surface.

TABLE 19

General Conditions	Order of Emergence	Time	Alligator No.	Cloacal Temperatures
Water temp., 39°–40° C.	1	3:18 P.M.	1}	39.0° C.
	2	3:18	2}	36.8
	3	3:20	4	37.0
	4	3:21	3	38.0
	5	3:26	5	38.0
	6	3:26	6	38.0

6. TOLERANCE TO COLD WATER

PURPOSE

This experiment may be regarded as the opposite of the preceding one. It was conducted in much the same manner as the Hot Water Experiment, but in this case the reaction of the alligators to cold water was determined.

How would alligators of varying sizes react to a constantly decreasing temperature? As in the other experiments, would the smallest individuals be the first to react to a lowering of the surrounding temperature to an unfavorable degree? Given the opportunity of voluntary adjustment to a constantly lower-

TABLE 20
FIRST TRIAL

General Conditions	Order of Emergence	Time	Alligator No.	Cloacal Temperatures	Temperature of Water	Notes
Sept. 4, 1944, afternoon Initial water temp., 28.2° C. Alligators in tank all morning, body temps. approximately same as water	1	2:15 P.M.	3	21.0° C.	18.0° C.	Put back in tank
	2	2:30	1	18.8	16.0	Put back in tank
	3	2:42	3	15.7	13.0	
	4	2:49	1	16.0	13.0	
	5	2:57	2	12.7	13.0	
	6	3:03	5	13.2	12.0	No. 5 taken out; put back
		3:13	3	31.2	—	Had been basking in sun; moved into shade
		3:17	2	—	—	Voluntarily returned to water
		3:19	1	33.8	—	Had been basking in sun; moved into shade
	7	3:20	2	19.5	12.0	
	8	3:22	5	12.2	12.0	Nos. 4 and 5 taken out, because they were obviously at a low stage of metabolism. No. 4 more active than no. 5. Both placed on sand, went into sun to bask
	9	3:24	4	11.9	12.0	
		3:34	2	25.5	—	Started to go into water
		3:34	4	17.5	—	Moved to shade
		3:39	5	21.0	—	Moved to shade
		3:49	—	—	14.0	All alligators basking in shade. Animals frightened, so that all except no. 1 returned to water
	10	3:58	3	16.8	—	
	11	4:07	4	16.6	—	
	12	4:12	2	16.0	—	
		4:25	5	—	—	No. 5 showed no inclination to leave water, so the trial was ended

ing temperature, how long would the animals withstand it? As in the preceding experiment, would the animals prefer to undergo unfavorable temperatures in an environment which to them seemed to be "secure" rather than to seek relief from low temperatures in "less secure" surroundings?

TECHNIQUE

The tank used in the preceding experiment was again used for this experiment. The alligators were placed in the tank with the water at air temperature, and they were allowed to remain in the tank under normal conditions for a time sufficient for them to

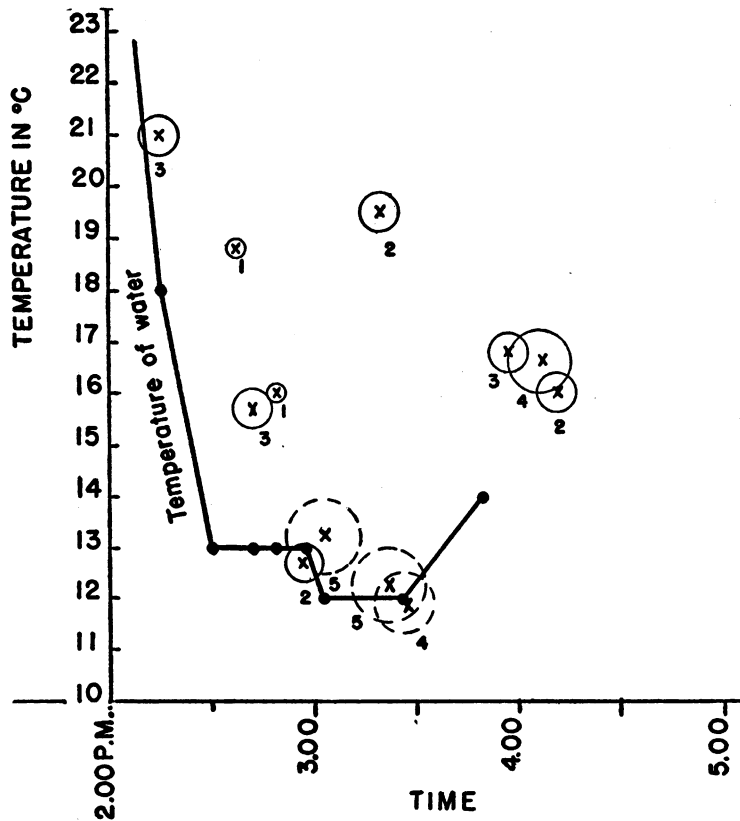


FIG. 13. Tolerance to cold water. First trial. Proportional body sizes, shown by circles, and the order of emergence indicated. Broken circles indicate alligators removed from tank, for the purpose of taking their temperatures, and then immediately returned to the tank. Numbers indicate the animals used. See table 20.

become accustomed to their surroundings. Large blocks of ice were then placed in the tank and the behavior of the alligators was observed. Records were kept of the order in which the animals left the tank, and as they came out their temperatures were taken. In the trials of this experiment the tank was open on top.

Alligators used in this experiment were nos. 1 to 5 inclusive, and, in addition, no. 6 during part of one trial. The reader is referred to page 335 for data as to the size and weight of these animals.

RESULTS

It was interesting to observe as a result of the first trial of this experiment that the al-

ligators evidently showed considerable tolerance to low temperatures. Whereas the range between what seemed to be the optimum and the critical maximum was one of but a few degrees, the tolerance for temperatures below the optimum was considerable, about 20° C. Moreover, it will be seen by table 20 that while the cold water finally forced the smaller alligators to emerge, the larger individuals remained and had to be removed forcibly. They were very sluggish when they were removed.

When these alligators first came out or were taken out of the cold water they were very cold and comparatively inactive. Their ability to regain heat after they had been in the sun was remarkably rapid, and it was a

TABLE 21
SECOND TRIAL

General Conditions	Order of Emergence	Time	Alligator No.	Cloacal Temperatures	Temperature of Water	Notes
Sept. 5, 1944, afternoon	1	1:27 P.M.	—	—	16.0° C.	
Initial water temp., 26.5° C.		1:31	2	16.2° C.	13.0	
Alligators all out of water, basking	2	1:34	2	—	—	Went into sun, then into shade
	3	1:36	3	14.3	12.5	
		1:40	1	12.5	10.5	
		1:46	1	—	—	Basking in sun
			3	—	—	
Initial alligator temps.:		1:53	4	—	—	At bottom of tank; very sluggish
No. 1, 33.8° C.			5	—	—	
No. 2, 31.7	4	1:55	4	12.2	10.5	Efforts to leave tank very feeble
No. 3, 32.5						
No. 4, 32.5	5	2:00	5	13.5	10.5	No. 5 taken out
No. 5, 32.5		2:03	1	32.6	—	Went out of sun into shade
Alligators then forced into water, to which ice had been added		2:03	3	30.5	—	Went out of sun into shade (substratum, 32° C.)
		2:12	1	34.0	—	
		2:18	4	25.2	—	Went out of sun into shade
						Back into sun
		2:31	4	29.8	—	Went out of sun into shade
		2:31	5	27.8	—	Went out of sun into shade
		2:31	2	32.0	—	Had been basking in shade
		2:31	—	—	—	Alligators forced back into water
	6	2:36	1	18.2	12.5	
	7	2:36	2	23.0	12.5	
	8	2:42	3	16.5	12.5	
		2:48	—	—	—	No. 6 put in tank
		3:12	—	—	14.0	
		3:31	—	—	16.0	Nos. 4 and 5 sluggish
	9	3:46	4	16.4	17.0	
		4:31	—	—	18.0	Increased activity on part of nos. 5 and 6
	10	4:57	5	18.6	19.0	
	11	7:16	6	21.0	21.5	No. 6 probably had been out for some time
						Trial concluded

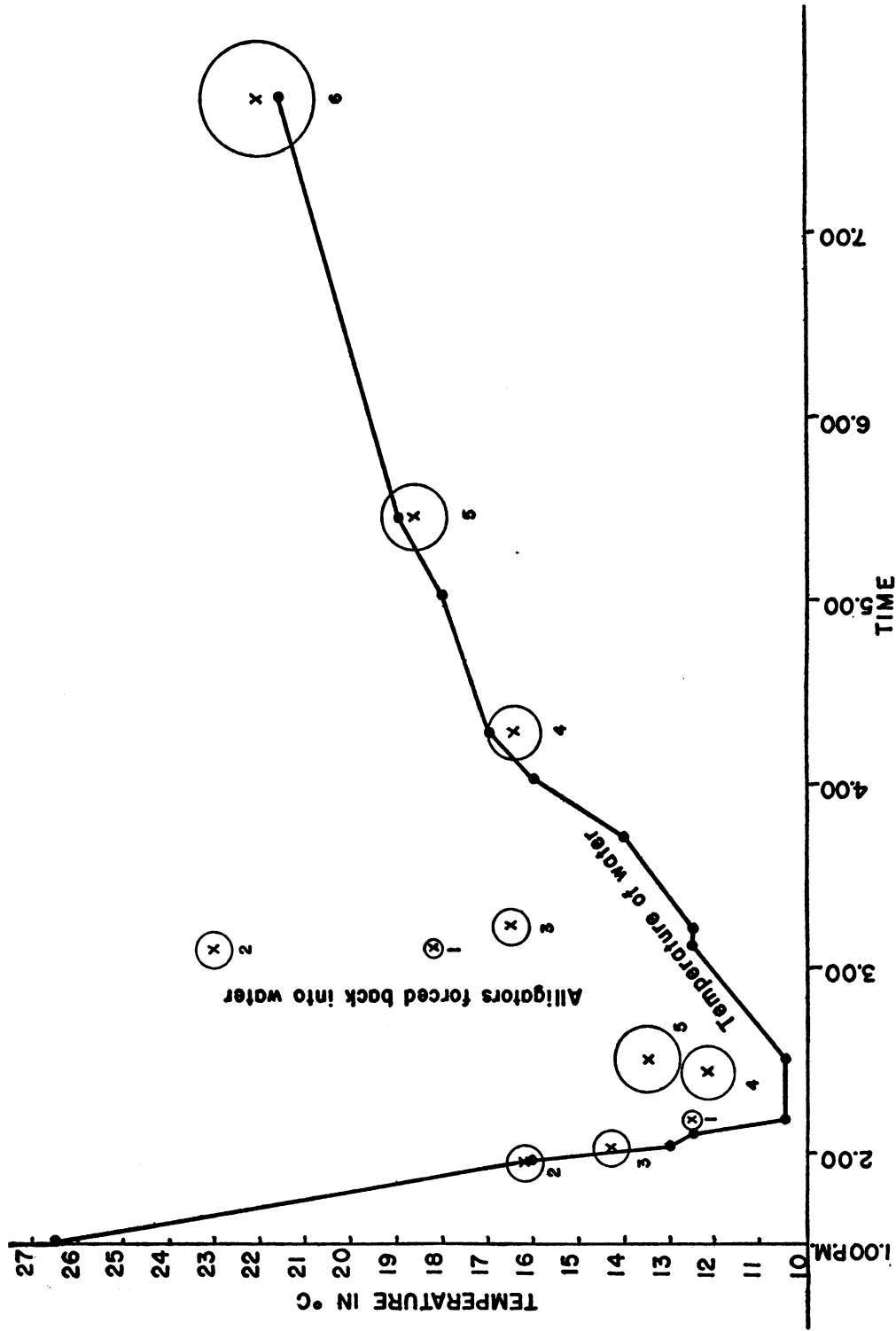


FIG. 14. Tolerance to cold water. Second trial. Proportional body sizes, shown by circles, and the order of emergence indicated. Numbers indicate the animals used. See table 21.

matter of but a few moments until they were completely restored to a state of more or less normal activity.

CONCLUSIONS

Alligators are affected much less severely by adverse conditions of cold for brief periods than they are by adverse conditions of heat. Moreover the degree of tolerance to low temperatures above freezing is greater and the limits to this tolerance are less sharply defined than is the case with high temperatures. In other words, these animals can withstand a drop of some 20° C. below the optimum temperature, whereas a rise of but a few de-

grees above this temperature is sufficient to be fatal.

For these reasons, the reactions of the alligators to low temperatures are much less marked than are their reactions to heat. In general the smaller individuals are first affected by the cold and are the first to react to this cold, but the reactions are not so completely correlated with size as in the case of reactions to high temperatures. In short, the alligator is better able to withstand adverse low temperatures above freezing than adverse high temperatures and presumably the same holds true for other crocodilians.

BEARING OF TEMPERATURE TOLERANCES IN THE ALLIGATOR ON HABITS, EVOLUTION, AND EXTINCTION OF THE DINOSAURS

AS ALREADY POINTED OUT in the introduction to this paper, the physiological reactions of modern crocodilians to variations in environment and temperature should give some clue as to what these same reactions might have been among dinosaurs exposed to similar environmental fluctuations. There are several reasons for making this assumption. In the first place, the modern crocodilians are archosaurian diapsids which in their taxonomic position are closer to the dinosaurs than are any other surviving reptiles. It is to be expected, therefore, that animals showing many morphologic similarities to the dinosaurs should also show physiologic similarities. Second, it is to be assumed that the crocodilians of our own day live in an environment not unlike the environment in which the dinosaurs lived; consequently a study of the responses of the recent animals to their natural surroundings should give some clue as to responses of the dinosaurs to the environment in which they lived more than 60 million years ago. Again, the crocodilians, being animals of some size, may offer a reasonably fair comparison with the dinosaurs, which were to a considerable degree giants in the adult state. Finally, it is possible by working with the crocodilians to get a comparison in the young and adults of a single species between very small animals and rather large animals. Therefore the physiologic responses, as governed by size, to the same external conditions may be studied upon a comparative basis.

In this regard, it might be said here that the results of our experiments in Florida are particularly illuminating in showing the differences that are the result of increase in size in *Alligator mississippiensis*. With differences of such magnitude that the largest animal of our series was about 500 times greater in mass than the smallest one, there was afforded considerable opportunity for studying the reactions to environment as affected by size. In view of the bearing of this study on the dinosaurs, it is to be regretted that we were unable to work with a really large crocodilian, say an

alligator of 15 to 18 feet in length. Such an animal would be perhaps 10 thousand times greater by weight than the smallest individual, and would be of such size as to approximate in actual bulk some of the smaller or medium-sized dinosaurs. It is virtually impossible in this day, however, to obtain such large individuals, and we can only look back regretfully to the past when monsters like this were not uncommon. Of course, if a crocodilian of such size were available, the difficulties of making temperature experiments would be great and can be best left to the imagination.

The difference in the rate of heat absorption of large and small alligators exposed to the effects of the sun's rays brings up the question of how this evidence may be applied to an interpretation of temperature tolerances in the dinosaurs. It is impossible to do more than speculate, but perhaps a certain amount of speculation upon this problem may be legitimate; at least it is interesting. Certainly, with the work on the alligators for a background, it is speculation with some basis on facts.

It has been shown that whereas a very small alligator, weighing about 50 grams, requires when exposed to the full effects of the sun but seven and a half minutes to raise the body temperature from 27° C. to 32° C., a large alligator, weighing some 13,000 grams, requires approximately 30 minutes to raise the body temperature from 28° C. to 32° C. In other words the rate of temperature increase in the small alligator is 1° C. every minute and a half, while the rate of temperature increase in the large alligator, an animal 260 times as great in body mass as the small alligator, is about 1° C. every seven and a half minutes. Continuing this line of reasoning, it would seem probable that in an adult ten-ton dinosaur, say an animal with a body weight of about 9 million grams, the rate of temperature rise would be very much slower than in the large alligator. Indeed, if the same difference in temperature rise as existed be-

tween the large and small alligators were applied to the dinosaur (an animal 700 times greater in body mass than the *large* alligator) then one may suppose that it would have taken more than 86 hours to raise the body temperature by 1° C. in the adult extinct giant. Although 86 hours may seem an inordinate amount of time to effect a degree's rise in body temperature, one must never lose sight of the fact that the mass of the adult dinosaur is so much greater than the mass of even the largest alligator that the difference is difficult to appreciate without benefit of figures such as these. In short, the bigger, fully grown dinosaurs of Mesozoic times individually had huge amounts of reptilian bulk, and this fact must be kept continually in mind when discussing the adult animals. It is also essential to keep in mind the fact that whether these animals started life in an egg or as small, newly born young, they would pass through sizes similar to those of the subadult alligators. It is equally imperative to remember that the survival of a species requires survival at the weakest or most vulnerable point in the life cycle of an organism, that is, from oögonia and spermatogonia through to the adult stage. From earlier analyses of data, it is reasonable to think that the reactions to temperatures of ectotherms of similar size, whether adults or not, would resemble those in modern alligators where changes are comparatively prompt and rapid in young individuals, but much retarded in the adults. Therefore one may assume that thermal changes in the larger dinosaurs would be immeasurably slowed down as growth progressed.

In fact, with a postulated rise in body temperature of only 1° C. in 86 hours, one is tempted to ask if adult dinosaurs were subjected in any way to the adverse effects of the sun's rays. This is a legitimate question, and the answer can be available only after consideration of many factors. For instance, of the 24 hours in a day, only a half are daylight at the equator, but in the "temperate" zones (where maximum recorded temperatures are 8°–12° C. higher than in the equatorial zone) there is a notable disproportion so that in the summer at approximately mid United States the ratio may be only nine hours of night to

15 hours of daylight. Thus it appears probable that during the summer season, outside of the tropical zone, the body temperature of a large reptile would represent cumulative increments of heat. As far as small reptiles are concerned, it will be recalled that while the younger alligators acquired heat very rapidly they lost heat rapidly, a condition that would apply equally to immature dinosaurs, thus rendering them particularly susceptible to the effects of high temperatures. The large alligators, on the other hand, while absorbing heat slowly, lost that heat at a relatively slow rate, from which it follows that in the large dinosaurs there probably would have been a heat increment taking place at least during the period between the vernal and autumnal equinox. Indeed, it will be remembered that in the larger animals, the cloacal temperature continued to rise after the animals, which had been in the sun for some time, were removed to the shade. This effect must have been greatly magnified in the dinosaurs, suggesting that at certain growth stages the cumulative effect of heat may have been particularly difficult to avoid. While heat absorption in these extinct beasts was slow, heat loss must also have been very slow. Therefore it is entirely within the realm of possibility that much of the heat absorbed during one day would be retained overnight during most of the summer months when there is an excess of sunlight over darkness, and it is conceivable that the animal would begin the following day's activities with an increment of temperature that had piled up during previous periods of daylight. Consequently it is reasonable to think that the temperature in the larger adult dinosaurs was held at a fairly high level because of the ability of the tremendous body masses to retain stored heat. In all probability these massive adult animals would have displayed seasonal changes, but they may have had relatively stable diurnal temperatures under some conditions.

Although the adults of large species may have benefited from a stabilization of diurnal temperatures, it appears probable that at some stage of growth they lost the advantages of small size and the consequent availability of abundant shelter and may have been exposed to the hazards of heat absorption and

slow radiation without the safety factor gained with increased age and mass. That is, it seems probable that, although the dinosaurs may have achieved an optimum mass, they may have been obliged to pass through stages in their growth that were unfavorable for survival.

The stabilizing effect of large mass and decreased surface area might have given to adult dinosaurs something of the characteristics of warm-blooded (endothermic) animals. For instance, is it unreasonable to suppose that temperatures in the larger adult dinosaurs, during their heyday at least, were held at or near the optimum? And being at this point, with few of the sudden rises and drops that so characterize small reptiles, would not these great animals have been able to maintain relatively high rates of metabolism, as compared with other reptiles? This factor, together with heat protection resulting from their bulk, might have favored their survival and accounted for their dominance.

This would not mean that adult dinosaurs were more or less independent of their environmental temperatures, as are the endothermic animals, but rather that they were characterized by fewer and smaller fluctuations in body temperature than is the case in smaller reptiles. Indeed, if the body temperatures in the adult dinosaurs were maintained more or less at the optimum level, it would be disadvantageous for these animals to be exposed to the sun for considerable lengths of time, because this would result in increments of body heat that would not be readily lost. Since there would have been a tendency in a tropical environment, and even more emphatically during summer in a tropical climate in the middle latitudes, for heat to be added in a cumulative manner without compensatory losses, the dinosaur in consideration of its own well-being must have been able to avoid making additions to its body temperature above the optimum level. If once an animal of the bulk of an adult dinosaur, or possibly of some intermediate stage in the case of still growing individuals, approached its critical maximum, there would be a very considerable amount of time involved in a retreat from that dangerous point; consequently, the effects of heat stored within the

body might be deleterious to a considerable degree. However, it is reasonable to suppose that adults of some of the largest species may have achieved a fairly complete thermal protection through favorable habits, orientation, posture, evaporation, and through their especially great mass with a proportionably smaller absorptive surface.

From the foregoing analysis, it seems reasonable to suppose that although the juveniles would prove to be as susceptible to high temperatures as alligators of comparable size, the adults of larger size might not have been affected so adversely by these temperatures. In fact, it is possible that with the body temperature at the optimum, in so far as compulsion to feed or to move in the open permitted, these animals instinctively avoided any actions or exposures that would tend to add an appreciable amount of stored heat to that optimum level. Thus it is very possible that the dinosaurs, either as adults or young, depending on age and size, might have been compelled to avoid prolonged exposure to the hot sun just as rigorously as do the larger modern lizards, snakes, chelonians, and crocodilians.

In view of these considerations, what might have been the habits of the dinosaurs as far as their reactions to outside temperatures were concerned? In this respect some allowances must be made for the environments in which the dinosaurs lived, and for their habitual postures. For instance, the reactions of the upland dinosaurs to external temperatures might have been different from the reactions of aquatic or swamp-living forms. Again, there might have been differences of reactions according to whether the dinosaurs were large or small, or adults or juveniles, and whether they were generally bipedal or generally quadrupedal animals.

It is reasonable to assume that wherever possible the dinosaurs spent much of their time in the shade, whether they were upland or aquatic, bipedal or quadrupedal animals. It would seem evident that the climate of the earth except for seasonal fluctuations in the proportions of night to day, was rather uniformly tropical and subtropical during much of the Mesozoic Era. Moreover under these conditions the disproportion between day and

night, irradiation and heat dissipation would be most unfavorable in the temperate zones. Aside from this important difference, over much of the earth's surface and during much of the extent of that geologic era there may have been no great fluctuations in temperature in different regions on the surface of the earth, although it must be reiterated that the absorption-radiation periods would vary with latitude. The air was probably warm and moist within the tropics, but the direct rays of the sun during the dry season might have resulted in unduly high body temperatures.

The summer months beyond the equatorial zone present conditions that are difficult to evaluate. Within the tropics, and at certain seasons in the "temperate" zone, the large bulky dinosaurs, having attained optimum temperatures, would presumably find it very easy to hold those temperatures day after day by means of comparatively short sorties into the sunlight. Therefore it is possible that these animals spent much of their time in the shade of large palm trees and other vegetation, with occasional excursions out into the open glades. It seems necessary to stress the fact that while beyond the tropical belt, both to the north and south, temperatures may have been no greater than in the tropics today, the prolongation of periods of absorption might more than double these for radiation or heat loss. This suggests a resulting moderate daily increment throughout the summer months, at least in areas lying north and south of the equinoctial zone.

The aquatic dinosaurs, or rather those living in swamps and along lake shores, animals such as the giant sauropods and the ornithopods, presumably would have been able to seek relief from unduly high temperatures in the same manner as do the modern crocodiles, namely, by retreat to the water. However, we know virtually nothing of the habits of the young, perhaps the most heat-vulnerable age, and it is possible that the maximum summer temperature of swamps and lake shores may have been high and thus directly or indirectly have had a deleterious effect. Although we have no information on the temperature of water in a tropical climate under conditions of a great disproportion of heat absorption to heat loss, it may be safe to assume that in the

summer months the maximum temperatures would at least exceed the maximum produced in the equatorial tropics where equinoctial conditions prevail. In the present-day tropics both lacustrine and marine water remains fairly constantly at 29°–31° C. Speculation on this point is unsatisfactory, but it seems improbable that, with much higher summer temperatures due to longer days and shorter nights, we would find aquatic temperatures paralleling those of today. The upland dinosaurs (many of the theropods, the armored forms, and the ceratopsians) would of necessity have sought the shelter of shade for relief from the direct rays of the sun, and any general reduction in the amounts of available shade would have produced especially unfavorable thermal conditions. We can only speculate on the possibility that there may have been competition for adequate shade and shaded sources of food.

The experiments performed with the alligators on frames (see figs. 5–8) indicate the difference in temperature rises that may have obtained in the bipedal dinosaurs as compared with the quadrupedal types. Thus it is very possible that the bipedal forms may have exercised a certain amount of temperature control by facing the sun, especially in the early hours of the morning and the late hours of the afternoon. In this way, because of the lesser amount of body surface exposed to direct sunlight with a consequent lesser amount of temperature rise, the theropods and ornithopods might have had somewhat prolonged periods of activity in the open, as compared with their quadrupedal contemporaries. For the carnivorous, predaceous theropods, particularly, this may have been an advantage of some consequence.

One thing seems fairly certain as the result of the experiments upon alligators, and that is the probable diurnal independence, among the larger adult dinosaurs, of substratum temperatures. In reptiles that are close to the ground, or that habitually rest upon the ground, substratum temperatures offer an important source for heat absorption. In the dinosaurs, whether they were bipedal or quadrupedal, this was not the case as long as they maintained these postures. Therefore, for at least part of the time these animals

were quite independent of warmth in the ground beyond the small amount received by radiation.

What are the bearings of these considerations upon the evolution of Mesozoic reptiles? We know that there was certainly a tendency towards giantism among these reptiles during Mesozoic time, a development that may have been brought about to some extent by equable conditions of environment. These giant ectotherms could have flourished only in an exceptionally warm climate. As shown above, large animals living in a tropical or subtropical climate of relative uniformity would have, because of the conservation of stored heat in large body masses, certain advantages that generally accrue to the endotherms. As also pointed out above, this may explain, in part, the success and the absolute dominance of the dinosaurs during the Mesozoic Era.

We now come to the very vexing problem of dinosaurian extinction at the end of Mesozoic times. How are the extinctions of Mesozoic reptiles to be correlated with temperature tolerances in these animals?

One of us has advanced the idea that the great extinction of reptiles at the end of Mesozoic times may have been caused in part by a rise in environmental temperatures to such a degree as to prove fatal in one way or another to the dominant animals of the late Cretaceous period (Cowles, 1939, 1940). It was suggested that the dinosaurs of late Mesozoic times very likely were dark-colored animals as are the modern crocodilians, an idea that is thoroughly in accord with the probabilities as based upon phylogenetic relationships. It was further suggested that had there been an increase in general environmental temperature toward the end of Cretaceous times, or a reduction in the size and prevalence of vegetation, or increased aridity and a consequent decrease in river, swamps, and lakes, then any or all of these effects might have been accompanied by a certain amount of rise in the average body temperatures of the dinosaurs. Increased aridity might be accompanied by more effective heating; thus the adult dinosaurs, being large, dark-colored animals with high capacities for heat absorption, might have achieved

high temperatures from this or the other factors. There is also the possibility that at some stage of life they or their young might not have been able to make the necessary physiological adjustments or to find the necessary environmental relief from these adverse conditions. It is not necessary to postulate great increase in climatic temperatures since most vertebrates operate close to their threshold of heat damage. Slight changes in the environmental temperature or in the amount of radiant energy deployed against the body, but far too small to be reflected by changes in the inorganic environment, could account for serious changes operating only within the organism. Presumably even such moderate changes might or might not be expressed by a clearly demonstrated northward extension of tropical and subtropical floras. Another one of us (Colbert) has objected to this theory on the grounds that there is not sufficient evidence afforded by paleobotanical or stratigraphical data to indicate any sharp or significant rises in temperature during the transition from Mesozoic to Cenozoic conditions of environment. In the Cretaceous period, tropical vegetation was abundant and extended to arctic regions. At the end of Cretaceous times there were epeirogenic uplifts which caused a reduction in low-lying swamplands and a gradual development of extensive uplands. But while there is no direct evidence for marked temperature changes, thermal conditions were certainly not those of the present time and in the long run it seems to be true that the equable conditions of Mesozoic very gradually gave way to the more rigorous environments of Cenozoic times. In view of all these factors, it seems doubtful to Colbert and Bogert that the extinction of the dinosaurs and other contemporary reptiles at the end of the Cretaceous period can be rightfully attributed to a rise in temperature beyond the upper tolerances of these animals.

More recently, Cowles (1944) has shown that at least some modern reptiles, while having comparatively high somatic heat tolerance, have, as do mammals and many other organisms, a distinctly lower germinal capacity to withstand high temperatures. Therefore, he has suggested that while there

may not have been sufficient rises in environmental temperatures to prove individually fatal, as far at least as the large adult dinosaurs and their contemporaries were concerned, nevertheless there may have been sufficient increases to produce sterility, thereby bringing about the extinction of great groups of Mesozoic reptiles in a secondary fashion. Such may have been the case. It is difficult to advance any definite arguments against this hypothesis, for it is probable that temperature fluctuations, and particularly rises in the average temperatures, were instrumental either directly or indirectly in the extinction of the dinosaurs.

On the other hand, we come up against the fact that the extinction of the dinosaurs, as is the case with all widespread extinctions in the paleontological record, is difficult to explain on the basis of any single factor. Two of the authors (Colbert and Bogert) believe it preferable to ascribe the extinction of the dinosaurs to multiple factors, such as changes in environment and, concomitantly, of food supply that went along with the uplifts that characterized the Laramide Revolution, increases or decreases in average temperatures, or the rise of the mammals, and their "displacement" of the reptiles as dominant forms; while one (Cowles) believes that this extinction was caused primarily by a rise in the average temperatures resulting in widespread dislocation of the previously existing pattern of life. These are all statements that must of necessity lie within the realm of speculation.

Reviewing the evidence in whole, it seems that animal extinctions are very complex phenomena, and it is probable that they are caused by the interaction of numerous factors; consequently they are not understood,

and it is possible that they will never be understood. We are continually baffled by questions that defy explanation.

Why was there such a widespread and sudden extinction of reptiles at the end of Mesozoic times? If conditions were such as to cause the demise of numerous lines of terrestrial reptiles, why did not some of the aquatic and especially the marine forms persist into the Cenozoic? Why was the extinction of dinosaurian and other reptilian orders so complete? Why should not some of the generalized species within these orders, especially the smallest and least-specialized forms, continue beyond the Cretaceous-Paleocene transition? Why did they not persist within the tropics until much later dates than elsewhere and become established again in the cooler Eocene? Since the extinction of the dinosaurs was complete, why did not this process extend to the contemporaneous crocodilians which were closely related to the dinosaurs and similar to some of them in habits? If the mammals are involved in this picture, why did they not begin to assume a role of dominance much earlier than they actually did? What, so to speak, "held the mammals back" during the Jurassic and much of the Cretaceous periods?

These are questions the answers to which may very likely never be satisfactorily elucidated. We do know that the extinction of the dinosaurs was sudden and complete. And if conditions of temperature were involved in this extinction, we do have from the work on the alligator some clues as to the factors that were involved in the relationships and the reactions of the large reptiles to rising and falling temperatures to which they were subjected.

SUMMARY

THIS REPORT DESCRIBES AN ATTEMPT to infer the reactions of extinct reptiles, especially the dinosaurs, to high temperatures as based upon reactions observed in the modern alligator. Thus it represents an experimental and observational approach to the solution of a problem which heretofore has remained in the realm of speculative discussion. To carry on the work, studies of temperature tolerances in a graded series of 13 alligators were made at the Archbold Biological Station, near Lake Placid, Florida.

Initially, the critical maximum temperature for *Alligator* was determined to be between 38° C. and 39° C. For all practical purposes, it was found that a temperature of 38° C. might be regarded as the critical maximum.

Exposure of a graded series of alligators to the direct rays of the sun showed the rate of heat absorption in these reptiles to be inversely proportional to the mass of the animal. The smaller the animal, the more rapidly its body temperature was raised when the alligator was exposed to the heat of direct sunlight. As a corollary to this, the rate of heat loss was also inversely proportional to the mass of the animal, being most rapid in the smallest individual and slowest in the largest alligator.

It was found that when subjected to conditions under which the alligators might choose the temperature most suitable to them, they showed a preference for conditions whereby their body temperatures were held at a point a few degrees below the critical maximum. That is, the optimum temperature for these reptiles seemed to be between about 32° C. and 35° C.

When animals of similar size were placed in postures like those maintained by the extinct dinosaurs and exposed to the heat of direct sunlight, it was found that there generally were differences in the rates of temperature increases in the several individuals. Thus, the alligator in a bipedal posture (similar to that of the theropod and some ornithopod dinosaurs) showed the slowest rate of increase in body temperature. This was due to the fact that a smaller area of the body was exposed to

the sun's rays than was the case in the other dinosaurs. Generally speaking, the alligator in a quadrupedal posture (similar to that of the sauropod, ceratopsian, and armored dinosaurs) was intermediate in its temperature increase. In this animal there was an increased surface area exposed to the direct rays of the sun, as compared with the bipedal animal, but there was an opportunity for circulation of air between the belly and the ground. The alligator flat upon the ground usually showed the most rapid rate of temperature increase, because this animal was receiving not only a large amount of sunlight on the surface of the body, but also was absorbing heat from the substratum.

An alligator exposed to a constant temperature at or near the critical maximum over periods of 12 and of 24 hours was able to maintain its body temperature at a point slightly below the environmental temperature which was virtually constant under experimental conditions. In doing this, however, the animal lost a large amount of weight (approximately 20 per cent in 24 hours) caused by the evaporation of body fluids. When placed in water, after such exposure to a high temperature, the animal quickly regained almost all its original weight.

A graded series of alligators was placed in water, the temperature of which was gradually increased to a point some degrees above the critical maximum of 38° C. The alligators preferred to stay in the water until their body temperatures had almost reached the critical maximum. They then left the water, and, generally speaking, the order of emergence was regulated by size of the individual. That is, the smallest animal which absorbed heat most rapidly was the first to leave the water, while the largest alligator was last to come out.

These alligators, when placed in water the temperature of which was lowered, showed a surprising degree of tolerance to cold. Whereas they could withstand temperatures only a few degrees above the optimum body temperature, they were able to withstand the lowering of environmental temperatures to

points 20 degrees or more below the optimum. Again, the reaction to these cold temperatures was a function of size, the smallest individual being the first to emerge from the cold water and the largest animal showing the slowest reaction to a cold environment.

How may these facts, observed in the alligator, be applied to speculations concerning the dinosaurs? Is a transference of facts regarding a living reptile to speculations regarding an extinct reptile valid? It is here considered to be valid because of (a) the close taxonomic relationship between the Crocodilia and the dinosaurs, (b) the probable similarity of environments in which crocodilians now live and in which the dinosaurs once lived, and (c) the fact that crocodilians are large reptiles, as were most of the dinosaurs.

From the observations of the reactions of alligators to high temperatures, it is reasonable to suppose that in the large, adult dinosaurs, the rise in body temperatures as a result of exposure to the heat of direct sunlight would be relatively slow, because of the great bulk of these animals. Conversely, the loss of temperature body heat in these animals also would be very slow.

Thus it might be possible for the dinosaurs, by regulating their exposure to the sun, to maintain a temperature at the optimum with no great amount of fluctuation up or down. Therefore these reptiles may for this reason have had some of the advantages of endothermic animals, and this may explain in part their absolute dominance as land animals over a period of more than 100 million years.

If such is the case, it is probable that the dinosaurs had habits of life that enabled them to maintain relatively constant, optimum temperatures. It may be that the upland forms sought the shade of trees during much of the daytime, while the lowland forms spent a greater portion of the daylight hours in swamps or lakes or rivers. The bipedal dinosaurs would be able to regulate the rate of temperature increase to some extent by facing the sun. This would be of particular advantage to the predatory theropods, which would as a result have somewhat longer periods of daytime activity than would the quadrupedal dinosaurs upon which they preyed.

It must be remembered, however, that

whatever the habits of the large, adult dinosaurs with regard to environmental temperatures, the young animals, during the earlier stages of their growth, would be subjected to all the deleterious effects of high temperatures to which all other small reptiles are subjected. But once the young had passed beyond the early stages of growth, theirs was the advantage of the large reptile with a rather constant body temperature probably maintained near the optimum.

Why did the dinosaurs become extinct? Cowles believes that the extinction of these great reptiles at the end of the Mesozoic Era may be explained by a rise in temperature which may not have been of sufficient magnitude to appear in the geologic record, but nevertheless was great enough to bring about the end of numerous lines of reptilian evolution. Perhaps the effect of such an increased temperature was felt only at certain stages in the growth of the individual. Even though limited, such an effect would, nonetheless, be fatal to the race. Or perhaps the effects of an increase of temperature were indirect rather than direct. Recently Cowles has shown that some modern reptiles have a relatively low germinal capacity to withstand high temperatures, even though the somatic heat tolerance may be considerable. Thus, a rise in environmental temperatures at the end of the Mesozoic may not have affected the individual somatically, but it may have been sufficiently great to prevent reproduction. Thus the race would be effectively cut down and in short order.

On the other hand, Colbert and Bogert feel that extinction is a complex phenomenon, hardly to be explained by changes in temperature alone. Other factors, such as changes in food supply, ecological competition brought about by the increase of the mammals, and the like, must be taken into account. These authors feel that there is much about the extinction of the dinosaurs that we do not understand, and the same is true of other extinctions throughout the geologic record.

For instance, why was the end of the Mesozoic so sudden? Why did not some of the great aquatic and marine reptiles persist into the Cenozoic? Why did all the dinosaurs, even the smallest forms, become extinct? Why did

the crocodilians persist? What "held the mammals back" during much of the Mesozoic time? The answers to these questions may never be known. But we do know that extinction during the Mesozoic-Cenozoic transition was relatively sudden and com-

plete, and if temperatures were involved in this extinction we feel that the study of heat tolerances in the alligator has afforded some clues as to the possible reactions of the dinosaurs to the changing temperatures to which they were subjected.

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